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Entomological studies from a high tower in Mpanga Forest, Uganda

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ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

Manuscript received 29th September, 1960

(Read 7th December, 1960)

With 2 Plates and 35 Text-figures

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I. INTRODUCTION

By A. J. HADDOW, PHILIP S. CORBET AND J. D. GILLETT

(*East African Virus Research Institute, Entebbe, Uganda*)

THE East African Virus Research Institute is concerned with the arthropod-borne viruses of man and animals in East Africa, and particularly with those which are transmitted by mosquitoes. The high steel tower, from which the studies here reported were carried out, was designed mainly for the study of biting Diptera which might be concerned in virus transmission, but workers in other fields have also found it suitable for their studies, some of which are included in the present series.

The first studies on the vertical distribution of biting Diptera in Africa were carried out almost concurrently in Kenya and Uganda. The results obtained in

banana plantations in the Semliki Valley, Uganda, were published by Haddow (1945*b*), those from the Kaimosi Forest, Kenya, by Garnham, Harper and Highton (1946) and those from the Semliki Forest, Uganda, by Haddow, Gillett and Highton (1947). Another interesting group of catches was carried out at this time in the Entebbe area by Dr. K. Goodner, a member of the International Health Division of the Rockefeller Foundation, but the results were not published and are available only in the annual reports of the Yellow Fever Research Institute, Entebbe.

The work in the Semliki Forest mentioned above consisted mainly of 24-hour catches with human bait carried out simultaneously at a number of levels above ground, with controls at ground level. These studies, made in 1944–45, were accompanied by observations on microclimate. It was found that, as in South America, certain species bite mainly in the canopy, others in the understorey and others at ground level. The highest station established was at 82 feet, in a semi-emergent tree, the platform being well above the main canopy level. Here, though the canopy species were reduced in abundance, they were still prevalent and at once the question arose as to whether there might not be a good deal of activity in the free air above the forest.

During the succeeding years numerous tree platforms were erected—40 in the Semliki Valley and 7 near Entebbe. Extensive studies were carried out, about five hundred 24-hour catches being made. Meanwhile the problem of activity above the forest remained unsolved, though it was becoming more and more obvious that it was one of major significance. Thus the males of certain important species are seldom or never found in nature, a finding paralleled by work in South America on the genus *Haemagogus*, where the males of certain species were never obtained except by rearing from larvae (Kumm, Osorno and Boshell, 1946). It was suspected that such males might be found in and above the canopy and that their incidence there might be investigated by light-trapping. A more important point was that, apart from some early references, almost nothing was known of the swarming of African mosquitoes with the exception of *Anopheles funestus* Giles (Harper, 1944) and *A. gambiae* Giles (Muirhead Thomson, 1948). It seemed likely that swarming might occur over emergent trees in the forest and that the crepuscular periods would be, as in the case of European species, the important times (*see, for example*, Marshall, 1938). Evening twilight was already known to be a time of great activity in many species (Kerr, 1933; Haddow, Gillett and Highton, 1947; Lumsden, 1952) and it was felt that, should swarming over the forest occur in this period, it might well be at a time at which dispersal of mosquitoes to surrounding areas might occur. Thompson (1953) has shown that in calm weather in woodland there is a slow, almost continuous interchange of air between the upper and lower levels. Wellington (1945), however, has pointed out that as tropical forest is darker than the surrounding landscape, very rapid radiation of heat occurs at canopy level after sunset. Thus, though air within the forest is almost a closed system by day, thermals may tend to develop over it at sunset, and these may help to carry small insects to considerable heights and distances. It is known that aphids are carried to great heights daily (*see, for example*, Johnson, 1953) and it has been shown that mosquitoes may also occur in the upper atmosphere to heights of at least 5,000 feet (Glick, 1939).

Apart from swarming activity it was felt that mosquitoes might leave the forest in response to the influence of environmental factors. It was known that at ground level the microclimatic boundaries of the forest may break down at certain times and under certain conditions, permitting sylvan species to move out into surrounding environments (Boshell and Osorno, 1944; Haddow, 1945*a*). Further, it had been shown that the microclimate of the forest canopy may not differ very greatly from that in the open air (Allee, 1926; Haddow, Gillett and Highton, 1947). Shannon (1931*a* and *b*) had pointed out that most metallic mosquitoes are diurnal, and Bates (1944) had shown that many of them are arboreal. He suggested that the coloration

was connected with life in an " unfavourable " (*i.e.* rather dry) environment and showed (1947) that *Haemagogus*—typical members of this arboreal group—survive best in rather dry air which is actually circulating. It seemed, therefore, that some of the arboreal and diurnal African mosquitoes which have metallic colours—such as *Aedes longipalpis* (Grünberg)—might well be able to " break the barrier " and rise above the forest. The question appeared to call for thorough investigation.

It was decided that a high tower with catching-platforms and climate stations at regular levels was required, but many years passed before funds could be obtained. Finally, with the aid of a grant from the World Health Organisation, work was begun and the tower (Plates I and II) was completed in 1958. It is constructed of steel, and has wooden platforms at ground level, 30 feet (in the understorey), 60 feet (in a dense part of the canopy), 90 feet (above the main canopy but in the zone of numerous emergent trees) and 120 feet (high above the main canopy and on a level with the tops of the highest emergent trees in its vicinity). Standard meteorological screens were set up at 6 feet and on platforms at 50 and 110 feet. From time to time series of thermohygrograph readings were carried out in these screens. It was not possible to keep the instruments running throughout the period of almost a year during which mosquito studies were in progress, but the series of recordings covered both dry and wet seasons. Run-of-the-wind anemometers were used to study wind flow at various heights (Part II, p. 258) and a visiting worker made studies on light (Part III). Unfortunately another visitor, who studied rainfall at various levels, did not realise that our intention was to publish the work all at one time and his contribution has appeared elsewhere (Hopkins, 1960). Bamboo pots for mosquito oviposition were attached to the tower at vertical intervals of ten feet from ground level to the top.

Much thought was given to the placing of the tower. For 14 years the Institute staff had been working in a small forest at Zika near Entebbe, and this seemed in many ways suitable. There were, however, certain difficulties and finally it was decided to build in the Mpanga Research Forest, west of Kampala. Some of the advantages were administrative, but the most important was that, as this forest is maintained for research by the Forest Department of the Uganda Protectorate, it was thoroughly known and mapped, and the plant ecology had been studied in considerable detail. Some blocks of the forest are used for particular research projects, others for exploitation in the normal way, and others again are maintained in a state of nature.

An admirably terse description of the forest has been given in a pamphlet circulated by the Forest Department (Ref. GPUP–2015–IM–8–55, Entebbe, May 1955) and it is felt that the writers cannot do better than quote this *verbatim* :

> " Position : 0°12′–13′N., 32°17′–18′E. 25 miles (40 km.) west of Kampala on Masaka road, about 10 miles (16 km.) north of Lake Victoria. Forest Reserve of 1,121 acres (450 ha.). Altitude : 3,800′ (1,160 m.). Climate : Rainfall mean about 45″ (1130 mm.), lowest recorded fall about 35″ (890 mm.) and highest about 66″ (1670 mm.) with 2 to 4 months of less than 2″ (50 mm.). Temperatures from 50°F. (10°C.) to 92°F. (33°C.), mean about 75° F. (24°C.). Relative humidities from 60 per cent. to 95 per cent. Topography : Level valley flanked by gentle slopes of low hills, draining N.W. to join the south-flowing Nakyetema swamp. Soil : Swamp : blue-grey heavy clays with some peat, pH. about 5. Slopes : deep lateritic red-earth with murram gravel over highly decomposed gneiss and quartzite, occasional ironstone outcrops, pH. 5 to 6. Forest Types : Swamp : permanently flooded or water-logged *Mitragyna-Macaranga-Phoenix* association with some *Erythrina* and *Spondianthus*, over *Euphorbia teke* and acanth-marantaceous herb layer with much *Dracaena laxissima*. Developed from *Cyperus papyrus* with all seral stages. Slopes : well developed *Celtis-Aningeria* association up to

160′ (50 m.) top height, rich in species of seral stages from *Pennisetum-Hyparrhenia* grassland, of the genera *Albizzia*, *Piptadenia*, *Lovoa*, over dense *Acalypha-Dracaena fragrans* shrub layer, over almost continuous *Leptaspis* ground layer. REFERENCES: Locality described by A. S. Thomas, *Journ. Ecol.* **33**: 24–30 (1945). Papyrus-forest sere by W. J. Eggeling, *Journ. Ecol.* **23**: 422 (1935)".

The site selected was in a swampy valley and the tower stands at the junction of swamp and slope forest. A small perennial stream flowing from a hill-foot seepage passes within a few yards of the base. During building the greatest care was taken not to cut trees or branches and to disturb the undergrowth as little as possible. The tower rises, itself like a forest tree, through a dense stand of timber in which *Pseudospondias microcarpa* (A. Rich.) Engle., *Erythrina excelsa* Bak., *Canarium schweinfurthii* Engl. and *Entandrophragma angolense* (Welw.) C.DC. are prominent. Slightly further down the valley wetter conditions lead to a dominance of *Pseudospondias*. Prominent among understorey trees is *Euphorbia teke* Schweinf. *ex* Pax, and the shrub layer is largely composed of *Dracaena fragrans* Ker-Gaul whose topmost axils provide a breeding-ground for mosquitoes of the genus *Eretmapodites*.

The tower was built beside a hugh tree (*E. excelsa*) as it was felt that this might provide a swarming focus. Actually, as will be described in Part V, the tower itself has proved to be a focus for swarming Diptera belonging to many different groups.

When first erected, the tower rose through a particularly dense patch of forest in which an important feature was an exceptionally heavy growth of lianas and of epiphytic ferns and orchids. It was considered that this dense concentration of plants in the canopy would give good harbourage for resting mosquitoes. Among the lianas, and forming a crucial support for the tangled mass, is one of exceptional size. At about 50 feet from its origin it is still over 30 inches in girth and its length the writers estimate as not less than 400 feet. It originally passed, close beside the tower, through the crown of three *Pseudospondias* of medium size. During a severe storm one of those was uprooted, and the other two now had to bear the immense weight of this liana, plus that of numerous other smaller specimens together with the masses of epiphytes with which they were covered. This proved too great a load and, after a few weeks, one of the *Pseudospondias* snapped off at about 12 feet above ground. The other fell subsequently, uprooted by the additional weight it now bore. The result was that the tower is now rather exposed on one side at understorey level though still closely surrounded on the others. In the outcome, no apparent difference in the catches was obvious. This agreed with past experience at Zika where on one occasion a large semi-emergent tree standing beside one of the platforms fell, bringing down many branches from other trees with it and leaving a considerable gap in the canopy. No change in the catch results was, however, apparent.

Before the tower was built, catches of various kinds were carried out in order to investigate the local fauna. Taken together with the subsequent work on the tower, the records of those collections have revealed the presence of a considerable number of species. Not all of these were common in the catches which will be described in greater detail in the subsequent papers that form parts of this series, and it is therefore convenient to give at this stage the complete list of biting Diptera taken in the Mpanga Forest at any time by Institute staff. The names are given in full in Appendix A to permit the use of abbreviated names in the following papers. The nomenclature of Stone, Knight and Starcke (1959) has been followed for mosquitoes as, though some of the names are not those generally used in the British Commonwealth, this is the only up-to-date and complete list available. Where contracted names have been employed, *Ae.* is given for *Aedes* to avoid confusion with *Anopheles*, which is given as *A.* Biting Diptera referred to below which are not known from Mpanga are listed in Appendix B. Certain other (non-biting) insect groups have

also been studied on the tower. These form the subject of separate papers in this series, in which the species are listed in full.

All the papers referred to in this and subsequent parts in the series have been combined in a single list at the end. When another paper in this series is cited in the text, it is referred to simply by its part number.

In mosquito catching our standard procedure is to adjust the clock so that 1800 hours " catch time " corresponds to the actual time of sunset. As Mpanga is very close to the equator, sunrise is very close to 0600 hours "catch time ".

The measure of central tendency used in these papers is the logarithmic transformation introduced by Williams (1937, 1939). Formerly it was usually referred to as " Williams' modification of the geometric mean ". This definition was considered to lack precision, and the term " Williams' Mean " (designated by the symbol M_w) is considered preferable (Haddow, 1960).

The term " circadian " is a recent one (Halberg, Halberg, Barnum and Bittner, 1959). Originally it implied a period differing from 24 hours by not more than a few hours. By most workers it is now taken to imply a period approximating to 24 hours.

In conclusion we wish to thank the many workers in different fields who contributed to the actual building of the tower, particularly Mr. J. D. Smithers of H. Young & Co. (East Africa) who designed it, Mr. B. C. Eccleston, Supervisor, Provincial Engineer's Office, Public Works Department, Uganda, who designed the foundations, Mr. F. W. Volrath, Transport Officer, Public Works Department, who solved a difficult transport problem for us and Mr. K. P. Dewar, also of the Public Works Department, who actually built the foundations. We are indebted to Mr. H. C. Dawkins, Ecologist, Forest Department, Uganda, for much information concerning the Mpanga Forest and for permission to quote the description printed above, and to Mr. D. J. Bargman of the East African Meteorological Department for help in installing and calibrating the recording instruments.

(*APPENDIX A* overleaf)

APPENDIX A

LIST OF BITING DIPTERA RECORDED FROM MPANGA FOREST

Species	Identified as: Males	Females	Larvae
CULICIDAE			
Anopheles (*Anopheles*) *coustani* Laveran *s.str.*	+	.	.
var. *ziemanni* Grünberg	+	.	.
implexus (Theobald)	+	+	+
obscurus (Grünberg)	+	+	.
(*Cellia*) *gambiae* Giles	.	+	.
Toxorhynchites (*Toxorhynchites*) *brevipalpis* Theobald subsp. *conradti* Grünberg	+	+	+
Malaya taeniarostris (Theobald)	.	.	+
Ficalbia (*Ficalbia*) *uniformis* (Theobald)	+	+	.
(*Mimomyia*) *hispida* (Theobald)	+	.	.
Mansonia (*Coquillettidia*) *aurites* (Theobald) group	+	+	.
fraseri (Theobald)	+	+	.
fuscopennata (Theobald)	+	+	.
maculipennis (Theobald)	+	+	.
metallica (Theobald)	+	+	.
pseudoconopas (Theobald)	+	+	.
versicolor (Edwards)	+	+	.
(*Mansonioides*) *africana* (Edwards)	.	+	.
uniformis (Theobald)	+	+	.
Uranotaenia alboabdominalis Theobald	+	+	.
balfouri Theobald	.	+	.
candidipes Edwards	.	+	.
chorleyi Edwards	+	+	.
hopkinsi Edwards	.	+	.
nigromaculata Edwards	+	+	+
pallidocephala Theobald	+	+	.
aff. *pallidocephala* Theobald	+	.	.
Hodgesia cyptopus Theobald	.	+	.
Eretmapodites chrysogaster Graham group	.	+	+
hightoni Someren	+	+	+
oedipodius Graham ssp. *parvipluma* Edwards	.	+	.
semisimplicipes Edwards	+	+	+
Aedes (*Mucidus*) *grahami* (Theobald)	.	+	.
nigerrimus (Theobald)	+	.	.
(*Finlaya*) *ingrami* Edwards	+	+	.
longipalpis (Grünberg)	.	+	+
(*Stegomyia*) *africanus* (Theobald)	+	+	+
apicoargenteus (Theobald)	.	+	+
dendrophilus Edwards	+	+	+
simpsoni (Theobald)	.	.	+
(*Aedimorphus*) *abnormalis* (Theobald) group	.	+	.
argenteopunctatus (Theobald)	+	.	.
capensis Edwards	+	.	+
cumminsii (Theobold)	+	+	.
domesticus (Theobald) *s.str.*	+	.	.
group	.	+	.
haworthi Edwards	+	.	.
leptolabis Edwards	+	.	.
aff. *mixtus* Edwards	+	.	.
mutilus Edwards	+	+	+
phyllolabis Edwards	.	.	+
tarsalis (Newstead) *s.str.*	+	.	.
group	.	+	.
(*Neomelaniconion*) *circumluteolus* (Theobald)	+	+	.
palpalis (Newstead)	+	.	+
taeniarostris (Theobald)	+	.	.
(*Pseudarmigeres*) *albomarginatus* (Newstead)	.	+	.

Species	Identified as : Males	Females	Larvae
Culiseta (*Theomyia*) *fraseri* (Edwards)	.	.	+
Culex (*Lutzia*) *tigripes* Grandpré and Charmoy	+	+	+
(*Neoculex*) *horridus* Edwards	+	.	.
insignis (Carter)	+	+	.
kingianus Edwards	+	.	+
(*Culiciomyia*) *cinerellus* Edwards	+	.	+
cinereus Theobald *uniformis* Theobald	+	.	.
macfiei Edwards	.	.	+
nebulosus Theobald	+	+	+
semibrunneus Edwards	+	+	+
(*Culex*) *annulioris* Theobald	+	+	.
aff. *invidiosus* Theobald	.	+	.
moucheti Evans	+	+	.
perfuscus Edwards	.	+	.
poicilipes (Theobald)	.	+	.
pruina Theobald	+	.	.
aff. *quasiguiarti* Theobald	.	+	.
trifoliatus Edwards	+	.	+
univittatus Theobald var. *neavei* Theobald	+	.	.
TABANIDAE			
Haematopota fusca Austen	+	+	.
patellicorne Enderlein	+	+	.
ugandae Ricardo	+	+	.
lamborni Oldroyd	+	.	.
furva Austen	.	+	.
Thaumastocera cervaria Séguy	+	+	.
Tabanus thoracinus Palisot de Beauvois	+	+	.
secedens Walker	.	+	.
Chrysops centurionis Austen	+	+	.
funebris Austen	.	+	.
Tabanocella perpulcra Austen	.	+	.

(*APPENDIX B* overleaf)

APPENDIX B

LIST OF BITING DIPTERA, NOT KNOWN FROM MPANGA, MENTIONED IN OTHER PARTS OF THE SERIES OF PAPERS

CULICIDAE

Anopheles (*Anopheles*) *labranchiae* Falleroni subsp. *atroparvus* Van Thiel.
claviger (Meigen).
(*Nyssorhynchus*) *aquasalis* Curry.
(*Cellia*) *cinereus* Theobald.
culicifacies Giles.
funestus Giles.
gambiae Giles var. *melas* (Theobald).
kochi Dönitz.
leucosphyrus Dönitz.
philippinensis Ludlow.
stephensi Liston.
superpictus Grassi.
vagus Dönitz.
Psorophora (*Grabhamia*) *confinnis* (Lynch Arribàlzaga).
Aedes (*Ochlerotatus*) *cantans* (Meigen).
caspius (Pallas).
communis (De Geer).
flavescens (Müller).
taeniorhynchus (Wiedemann).
(*Stegomyia*) *aegypti* (Linnaeus).
vittatus (Bigot).
Culiseta (*Climacura*) *melanura* (Coquillett).
Culex (*Culex*) *bitaeniorhynchus* Giles.
pipiens Linnaeus.
salinarius Coquillett.
theileri Theobald.
univittatus Theobald.

SIMULIIDAE

Simulium damnosum Theobald.
ornatum Meigen.

CERATOPOGONIDAE

Culicoides nubeculosus Meigen.
pallidicornis Kieffer.
utahensis Fox.

TABANIDAE

Tabanus americanus Forster.
bishoppi Stone.
giganteus De Geer.
sulcifrons Macquart.
Chrysops dimidiata Wulp.
silacea Austen.

PLATE I

The 120-foot steel tower in the Mpanga Forest, Mengo District, Uganda.

PLATE II

The 120-foot steel tower in the Mpanga Forest, Mengo District, Uganda. (*Photo, Prof. A. W. Woodruff*)

The 120-foot steel tower in the Mpanga Forest, Mengo District, Uganda.

The 120-foot steel tower in the Mpanga Forest, Mengo District, Uganda.
(*Photo, Prof. A. W. Woodruff*)

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

II. OBSERVATIONS ON CERTAIN ENVIRONMENTAL FACTORS AT DIFFERENT LEVELS

By A. J. Haddow and Philip S. Corbet

(*East African Virus Research Institute, Entebbe, Uganda*)

The steel tower on which this work was carried out has been described, and an outline of the main investigation has been given in Part I of this series. The object of the present communication is to present the results of observations on temperature, humidity, wind force and wind direction made on the tower in the period 1958–59. The original programme made provision for a series of light-measurements, to be made, at the same time, with extremely sensitive photometers. As there was a delay of over a year between the time when these instruments were ordered and their final delivery at Entebbe, they arrived too late for use during the work here reported. Fortunately, a visiting worker was able to carry out studies on light at a later date (Part III).

Up till the present, the number of independent investigations on the microclimate of rain-forest has been limited, and the excellent summary of this subject given by Richards (1952) reveals that in many cases the periods covered by the observations concerned have been very brief indeed, even the results for single days being quoted in some cases. In the present study the results are based on fairly extended series of records. The work on microclimate was carried out at intervals over the better part of a year and covered both wet and dry periods.

In previous work in the Semliki Forest in Western Uganda (Haddow, 1945*a*) it was shown that the climate near the ground within the rain-forest is very much cooler, moister and more equable by day than that in the open air at the same level, and it is further known that by day, in calm weather, the air in woodland is virtually a closed system, with a slow almost continuous interchange between the upper and lower levels (Thompson, 1953). By night, however, these differences largely disappear and the microclimatic barriers between forest and the open air tend to break down. Consequently, in equatorial Africa, sylvan mosquitoes may infiltrate areas adjacent to the forest by night (Haddow, 1945*a*), and in this connection it is interesting to note that in South America, also, forest-dwelling mosquitoes (of the genus *Haemagogus*, which are important yellow fever vectors) may move outward from the forest edges in the late afternoon (Boshell and Osorno, 1944).

Subsequent observations in the Semliki Forest carried out by Haddow, Gillett and Highton (1947) were concerned mainly with the vertical stratification of the microclimate. These showed that where temperature and humidity were concerned there was a considerable difference between the conditions found near ground level and those obtaining in the understorey, but relatively little between those in the understorey and those in the canopy. It was further pointed out that conditions in the understorey and canopy did not differ greatly from those found in the open air. It is interesting to note that Allee (1926) had found a similar state of affairs in the Barro Colorado Forest in Panama. This is not mentioned explicitly in his text, but is clearly implied by his graphs. Bates (1944), discussing the Colombian rain-forest, states that his results were in close agreement with those of Allee, but afterwards says that humidity and temperature changed gradually with height, in which case

it would appear that they differed from Allee's results in at least one important particular.

Though to a certain extent each forest may present an individual picture where temperature and humidity are concerned—and this applies particularly to vertical gradients—all workers are agreed that, in the canopy, conditions are much drier than those near ground level. Many canopy mosquitoes have metallic colouring, and it has been suggested by Bates (1944) that such colouring may be associated with a relatively dry environment of this type. He has further shown (1947) that in the laboratory the highly metallic *Haemagogus spegazinii falco* Kumm, Osorno and Boshell—a canopy species—requires relatively dry air, preferably circulating, for satisfactory survival. The importance of vertical stratification has been very clearly demonstrated by the classic studies of Pittendrigh (1950*a* and *b*) on malaria in Trinidad. Here humidity, and particularly its vertical stratification, was shown to have a dominant influence on the distribution of the main anopheline vectors, which breed in bromeliads.

In all the work described above, the zone above the forest has been largely ignored, and it was considered a matter of prime importance to investigate it. One of the main objects of the study was to determine whether there is by day a microclimatic barrier between the forest canopy and the zone above it, and whether by night this barrier breaks down, permitting sylvan mosquitoes to rise above the trees.

During the work Lambrecht thermohygrographs were set up in Stevenson Screens of standard size at " ground level " (actually 6 feet), and on the platforms at 50 and 110 feet. It was not possible to place the instruments on the catching platforms at 60 and 120 feet because the screens occupy too much space. As, however, the legs of the screens were fairly long, the actual instruments were approximately 6 feet above the platforms concerned, and so only 4 feet below the levels at which catches were made. Thus the uppermost instrument was placed at approximately 116 feet, in a zone above all but the largest of the emergent trees, the middle instrument at about 56 feet, in a dense part of the canopy, and the lowest one at about 6 feet, just above the lower shrub-layer, here composed mainly of small *Dracaena* plants. The anemometers were standard 5-inch-cup run-of-the-wind instruments. Being fairly compact, these were mounted on metal brackets on the safety rails surrounding the 120-foot and 60-foot catching platforms. The third instrument was placed on top of the ground-level thermometer screen, and was thus approximately 6 feet above the actual forest floor. In the rest of this paper these three main zones will be referred to, for convenience, as " above the canopy ", " canopy " and " ground level ".

It is extremely difficult to maintain meteorological instruments in good running order in rain-forest, and in the present case many days' readings were lost. With six pens writing the temperature and humidity records, breaks in the line and blots frequently occurred, particularly when stormy conditions caused the tower to sway slightly, and in such cases the records for the 24-hour period were discarded. A 24-hour period was accepted for inclusion only where all 6 records were clearly legible throughout. In the course of the work there were altogether 46 such complete 24-hour periods. On these are based the conclusions reached below.

Wind direction was read hourly during 24-hour catches, the reading always being made on the 120-foot platform. There are 42 complete sets of such readings. Where wind flow was concerned, the available series is much shorter. Readings were made hourly at all three levels during 24-hour catches, but only the first 18 catches provided acceptable results, as after this some of the instruments became defective, the main trouble being corrosion (possibly due to bacteria) in the ball-races. Spare parts arrived too late to be useful. The 18 complete 24-hour cycles of readings do, however, show a clear and easily understood pattern.

Before detailed discussion of the results it should be noted that, throughout the work, time was adjusted so that 1800 hours corresponded with the actual time of

sunset. As the Mpanga Forest is situated within a few miles of the equator, both day and night are of approximately 12 hours' duration throughout the year.

TABLE I.—*Mean temperatures (°C) Mpanga Forest, near ground level, in the canopy and above the canopy. Forty-six days' observation.*

	Weather					
	28 days with no afternoon rain			18 days with afternoon rain		
	Level (feet)					
	6	56	116	6	56	116
06–07	17·3	16·8	17·4	16·9	16·6	17·3
07–08	17·7	17·4	18·4	17·5	17·1	18·4
08–09	18·7	18·9	20·3	18·6	18·6	20·3
09–10	20·3	21·4	22·7	20·0	20·5	22·2
10–11	21·7	23·2	24·0	21·1	22·2	23·1
11–12	23·3	25·1	25·7	21·9	23·4	23·7
12–13	24·3	25·9	26·2	22·1	23·2	23·7
13–14	24·7	26·3	26·4	22·0	23·1	23·6
14–15	24·7	26·2	26·4	21·3	22·3	22·3
15–16	24·3	25·8	26·1	20·7	21·5	21·7
16–17	23·8	25·4	25·5	20·3	20·9	21·5
17–18	22·7	24·3	24·7	19·9	20·4	20·5
18–19	21·5	22·6	22·6	19·3	19·8	20·1
19–20	20·2	20·8	20·9	18·9	19·1	18·9
20–21	19·2	19·7	19·9	18·4	18·5	18·3
21–22	18·4	18·9	19·0	18·0	18·0	18·0
22–23	18·0	18·2	18·5	17·5	17·5	17·8
23–24	17·6	17·7	18·2	17·2	17·1	17·3
00–01	17·4	17·3	17·9	17·0	16·8	17·2
01–02	17·2	17·1	17·7	17·0	16·7	17·2
02–03	17·1	17·1	17·7	16·9	16·7	17·3
03–04	17·0	16·9	17·5	16·9	16·7	17·1
04–05	17·1	16·9	17·4	16·7	16·5	17·0
05–06	17·3	16·7	17·2	16·8	16·6	17·0
Absolute maximum	28·5	29·5	29·5	28·0	27·5	28·0
minimum	14·0	14·0	14·5	14·5	15·0	15·5
Range	14·5	15·5	15·0	13·5	12·5	12·5
Mean maximum	24·7	26·3	26·4	22·1	23·4	23·7
minimum	17·0	16·7	17·2	16·7	16·5	17·0
Range	7·7	9·6	9·2	5·3	6·8	6·7

TEMPERATURE

In the area in which the Mpanga Forest lies, afternoon rain is of frequent occurrence, and study of the temperature records has revealed that this is the most important single factor affecting the form of the temperature curve for any given day. Rain in the morning or during the night does not have an after-effect of the same magnitude or duration, and even seasonal differences are much less marked in this area than are those between days with, and days without, afternoon rain. So pronounced is the effect that the form of the curve produced by taking the mean of a series of days' readings will obviously depend very largely on the number of days on which rain is recorded during the afternoon. Accordingly, the sample has

been divided into two groups on this basis, and is made up of (*a*) 28 days with no afternoon rain and (*b*) 18 days with afternoon rain.

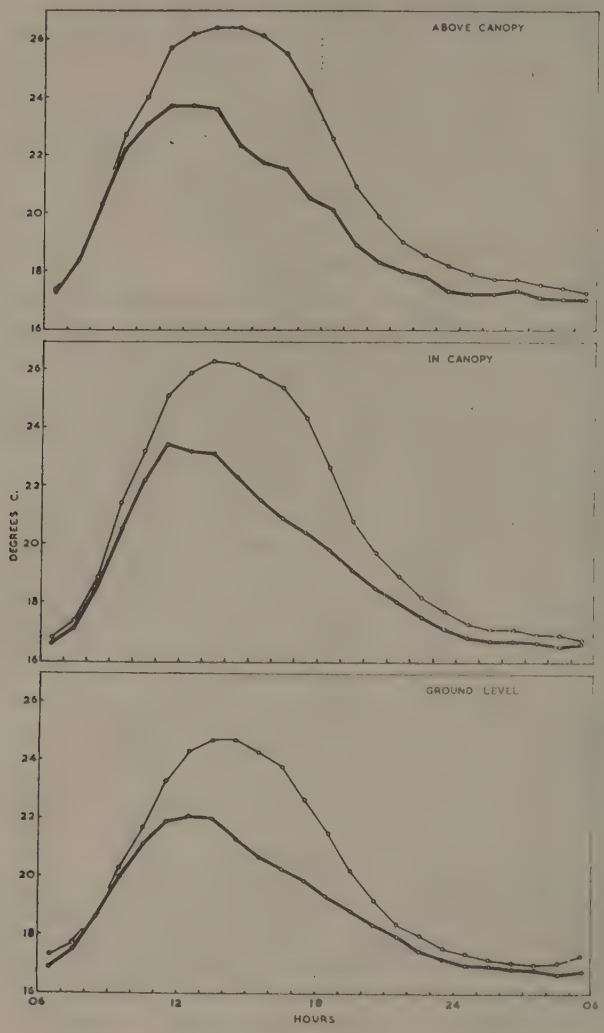

Fig. 1.—Mean hourly temperature (°C.) on 18 days with afternoon rain (thick line) and 28 days with no afternoon rain (thin line). The levels shown are : above canopy (116 feet) ; canopy (56 feet) ; ground level (6 feet).

The figures discussed below (Table I ; figs. 1 and 2) are means and show the general trend. As, however, afternoon rain does not begin at a fixed time, there is a pronounced smoothing effect, and the rather dramatic nature of the changes which may be seen on a single particular day is not apparent. They may, however, be mentioned briefly before the discussion of the main results. A heavy afternoon shower

brings about a fall in temperature, which may be as much as 9°C. above the canopy, 8°C. in the canopy and 5°C. at ground level and which may occur within 15–30 minutes. This sharp drop affects all levels more or less in the same way but subsequently each level follows a different course. Above the canopy, the rain being over, the temperature rises once more, probably almost to its former level. In the canopy some recovery occurs but the temperature remains at a lower level than before the rain. Near the forest floor little or no recovery takes place, and the temperature remains at a low level till the following day.

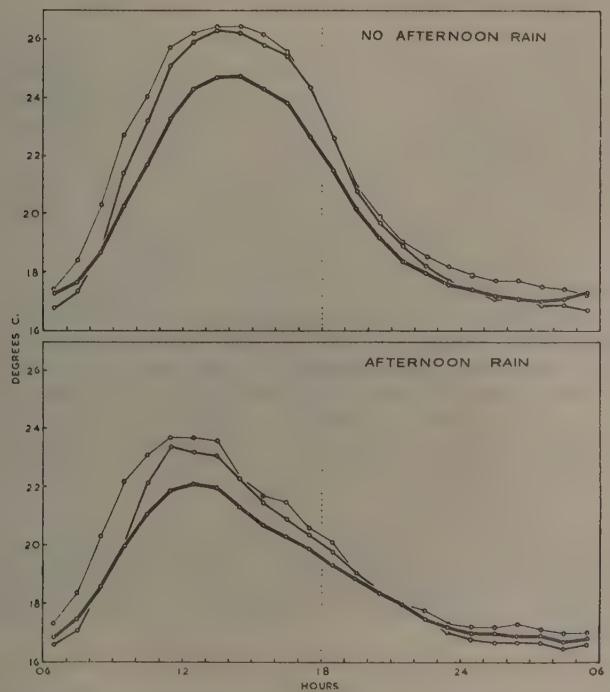

FIG. 2.—Mean hourly temperatures (°C.) on 28 days with no afternoon rain (top figure) and 18 days with afternoon rain (bottom figure). Thick line—6 feet (ground level); medium line—56 feet (canopy); thin line—116 feet (above canopy).

When the mean results are considered, it is at once seen that in the early morning there is no significant difference between the groups of days at any level. On days with no afternoon rain, temperature continues to rise till the period 14–15 hours, after which there is a fairly rapid fall till the early night and a more gradual fall thereafter till the hours before sunrise. On days with afternoon rain, however, gathering cloud has arrested the rise of temperature by midday, and thereafter there is a short "plateau" lasting for about two hours, followed by a rapid fall, brought about by the rain. It is thus in the period from midday till late afternoon that the great difference between the two groups of days occurs. The greatest mean difference shown in the present series between the groups is 3·6°C. at ground level, 4·5°C. in the canopy and 4·4°C. above the canopy.

The difference between the two groups of days is perhaps most clearly shown when

an arbitrary threshold temperature is taken and when the number of hours during which this threshold was attained or exceeded is compared for the two groups by level. If 22°C. be selected as a suitable threshold value (being the lowest which will show positive results at all levels) the following results are obtained.

Level (feet)	Number of hours during which a temperature of 22° C. was attained or exceeded	
	Days with afternoon rain	Days without afternoon rain
6	2	7
56	5	9
116	6	10

When a comparison is required between the trends at different levels, it is necessary once again to recognise the two groups of days (Table I; fig. 2) and it is at once apparent that the differences are of a relatively minor order, whether afternoon rain occurred or not. In neither of the two groups of days is there any significant difference between the 6-foot, 56-foot and 116-foot levels during the night and even during the hottest part of the day the differences are not great. At this time there is not much to choose between the canopy and the zone above it, but there is a clear difference of almost 2°C. between these two levels and the ground-level trace on days with no afternoon rain and of about 1·5°C. on days with afternoon rain. An inspection of the absolute and mean maxima, minima and ranges (Table I) shows how small the differences are—a most unexpected result in view of previous observations in the Semliki Forest, where the differences between ground level and the canopy even by night were as great or greater than those found in the hottest part of the day at Mpanga. Once again degree of difference is perhaps best shown by a comparison between the times at which an arbitrary threshold temperature was attained or exceeded. This may be gauged by reading the small text table, given above, vertically instead of horizontally.

The general conclusion is thus that the difference between days with and without afternoon rain is more important than the difference between levels or even seasons where the Mpanga Forest is concerned and further that, by night, there is no temperature barrier opposing the diffusion of mosquitoes upward through the forest into the air above the canopy.

Humidity

In the case of this highly important environmental factor it is considered that the use of relative humidity figures is frequently misleading. Saturation deficiency (which gives a good index of the drying power of the air) is much to be preferred, as it is to this particular characteristic of the atmosphere that the humidity responses of the mosquito are probably attuned.

Since the days for which figures are available are the same as those for which complete temperature records were obtained, it is necessary to subdivide them into the same two groups—28 days with no afternoon rain and 18 days with afternoon rain. The results are given (in mm. of mercury) in Table II and in figures 3 and 4.

The picture is very similar to that obtained in the case of temperature but the differences are even more pronounced. In the same way the rise of saturation deficiency is arrested early and falls abruptly on days with afternoon rain whereas in the other group of days it continues rising till well after noon. Once again the largest mean differences occur in the afternoon, namely 6·1 mm. at ground level, 8·0 mm. in the canopy and 7·9 mm. above the canopy and, as in the case of temperature, the differences between the two groups of days are quite insignificant in the early morning and at night.

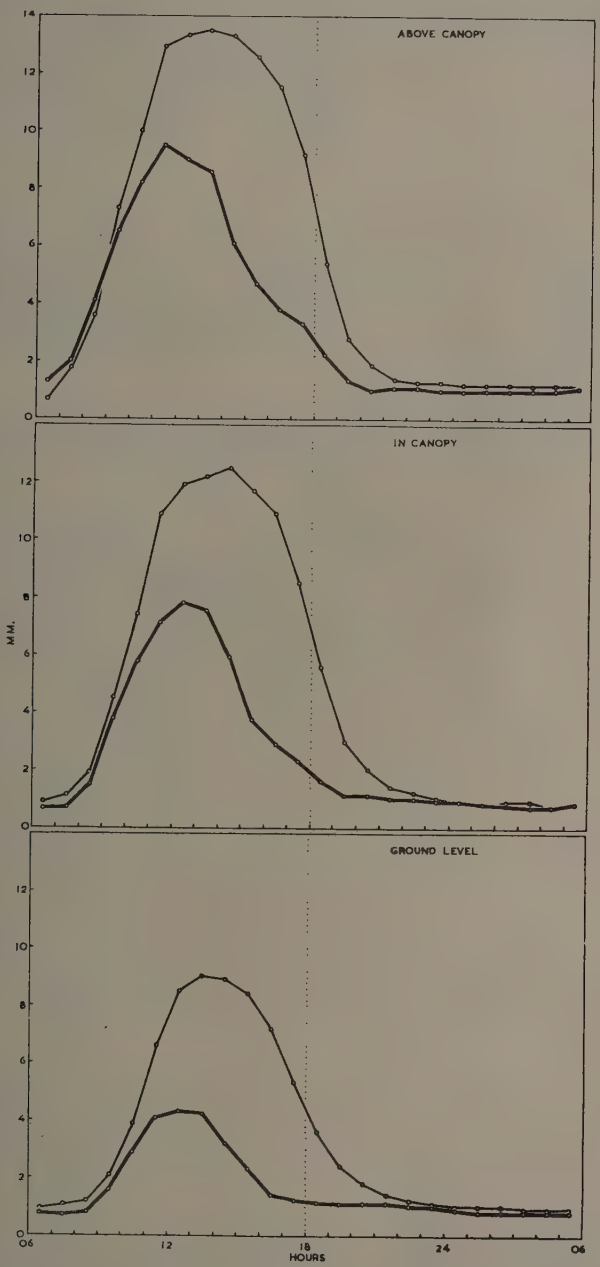

Fig. 3.—Mean saturation deficiency (mm. of mercury) on 18 days with afternoon rain (thick line) and 28 days with no afternoon rain (thin line). The levels shown are : above canopy (116 feet) ; canopy (56 feet) ; ground level (6 feet).

If an arbitrary threshold value of 4 mm. is accepted, the comparison between the two groups of days is as follows:

Level (feet)	Number of hours during which saturation deficiency of 4 mm. was attained or exceeded	
	Days with afternoon rain	Days without afternoon rain
6	3	7
56	5	10
116	8	10

When the three levels are compared (Table II; fig. 4) it is again apparent that no significant differences exist between them in the early morning or at night in the case of either group of days. Differences between the canopy and the air above it are, once more, surprisingly small. Thus the highest mean difference between the canopy and the air above it was only 2·7 mm. on days with afternoon rain and 2·8 mm. on days without.

TABLE II.—*Mean saturation deficiency (mm.) Mpanga Forest, near ground level, in the canopy and above the canopy. Forty-six days' observation.*

	Weather					
	28 days with no afternoon rain			18 days with afternoon rain		
	Level (feet)					
	6	56	116	6	56	116
06–07	0·9	0·9	0·7	0·8	0·7	1·3
07–08	1·1	1·1	1·8	0·7	0·7	2·0
08–09	1·2	1·9	3·6	0·8	1·5	4·1
09–10	2·1	4·5	7·3	1·6	3·8	6·5
10–11	3·9	7·4	10·0	2·9	5·8	8·2
11–12	6·6	10·9	12·9	4·1	7·1	9·5
12–13	8·5	11·9	13·3	4·3	7·8	9·0
13–14	9·0	12·2	13·5	4·2	7·5	8·6
14–15	8·9	12·5	13·3	3·2	5·9	6·1
15–16	8·4	11·7	12·6	2·3	3·7	4·7
16–17	7·2	10·9	11·5	1·4	2·9	3·8
17–18	5·3	8·5	9·2	1·2	2·3	3·3
18–19	3·6	5·6	5·4	1·1	1·6	2·2
19–20	2·4	3·0	2·8	1·1	1·1	1·3
20–21	1·8	2·0	1·9	1·1	1·1	1·0
21–22	1·4	1·4	1·4	1·1	1·0	1·1
22–23	1·2	1·2	1·3	1·0	1·0	1·1
23–24	1·1	1·0	1·3	1·0	0·9	1·0
00–01	1·0	0·9	1·2	0·9	0·9	1·0
01–02	1·0	0·9	1·2	0·8	0·8	1·0
02–03	1·0	0·9	1·2	0·8	0·8	1·0
03–04	0·9	0·9	1·2	0·8	0·7	1·0
04–05	0·9	0·8	1·2	0·8	0·7	1·0
05–06	0·9	0·8	1·2	0·8	0·8	1·1
Absolute maximum	17·9	22·3	23·9	12·4	15·7	17·2
minimum	0·1	0	0·1	0	0	0·1
Range	17·8	22·3	23·8	12·4	15·7	17·1
Mean maximum	9·0	12·5	13·5	4·3	7·8	9·5
minimum	0·9	0·8	0·7	0·7	0·7	1·0
Range	8·1	11·7	12·8	3·5	7·1	8·5

There was, however, a substantial difference by day between the ground-level results and those for the other two levels. Thus on days with afternoon rain mean differences as great as 3·5 mm. are recorded as between ground level and the canopy, and 6·3 mm. as between ground level and the air above the canopy. In the case of the other group of days the corresponding figures are 4·4 mm. and, once again, 6·3 mm.

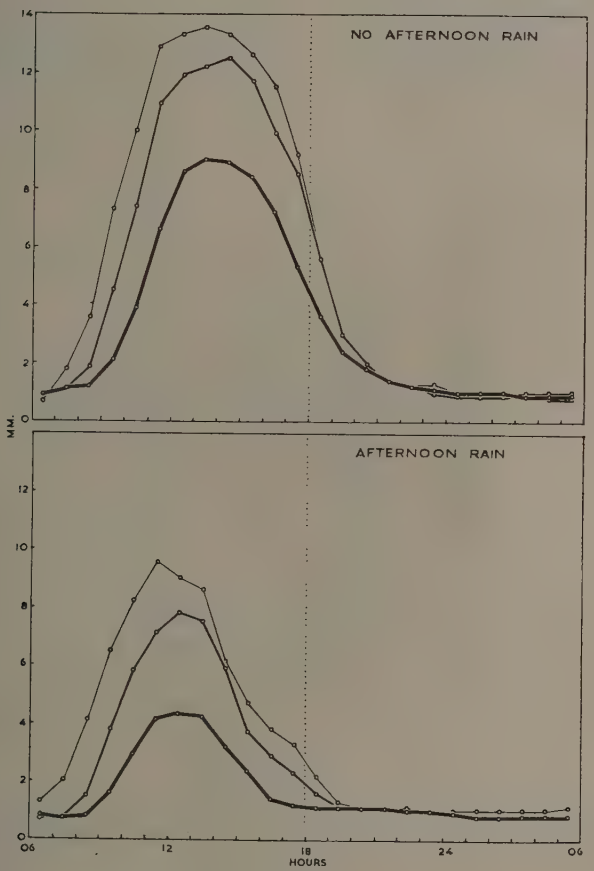

Fig. 4.—Mean saturation deficiency (mm. of mercury) on 28 days with no afternoon rain (top figure) and 18 days with afternoon rain (bottom figure). Thick line—6 feet (ground level); medium line—56 feet (canopy); thin line—116 feet (above canopy).

The durations of the periods during which each level attained or exceeded the arbitrary 4 mm. level here discussed are shown in the text table above.

As in the case of temperature, therefore, the differences between days with and days without afternoon rain are much more important than are those between levels or seasons and, once again, the humidity gradient presents no barrier to the diffusion of mosquitoes upward into the air above the forest by night.

Wind Direction

In some areas on or near the northern shore of Lake Victoria there is a regular daily off- and on-shore breeze cycle. As the Mpanga Forest lies within a few miles of the lake it was therefore considered worthwhile to investigate wind direction at all times of the day and night. The main object was to establish whether wind blew from the vast swamps bordering the lake in this area at times when swamp-breeding mosquitoes might be expected to migrate.

Hourly readings were therefore made on the 120-foot platform during all 42 of the 24-hour catches. When there was not enough wind to indicate direction, a zero return was made. The results (fig. 5) show that southerly winds predominate at all times of the day and night, with south-westerly winds next in order of prevalence. The different sizes of the polygonal " wind roses " in this figure reflect the numbers of positive and zero readings in the different periods.

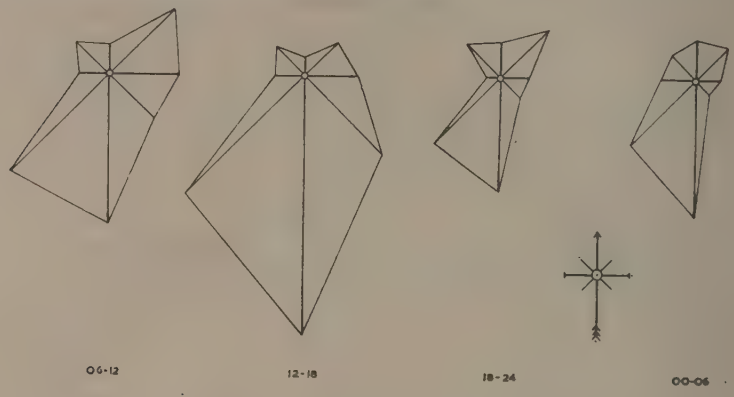

Fig. 5.—The distribution of wind direction by day and by night during forty-two 24-hour periods during which hourly records were made.

At all times, therefore, winds blowing from the general direction of Lake Victoria and its fringing swamps prevail in the Mpanga area, and these may well assist the downwind migration of swamp-breeding mosquitoes such as *Mansonia* spp.

Wind Flow

There is little available information on the wind flow at different levels in and above tropical rain forest, apart from the observations of Allee (1926), who showed that in the Barro Colorado Forest the ratio of wind flow at 75 feet to that at 6·5 feet was approximately 10 : 1. From an instrument at Gatun he estimated that the ratio of wind flow above the canopy : flow in the canopy : flow near ground level was of the order 240 : 24 : 1. The ratios found at Mpanga, though slightly less pronounced, still show an extremely steep gradient between 120 feet and 6 feet. As mentioned above, records were kept hourly during eighteen 24-hour catches. The total flow in these 24-hour periods (Table III) showed a ratio of 107 : 15 : 1 for the 120-, 60- and 6-foot levels. The anemometers, however, remained *in situ* and recording during the entire period over which these catches were scattered, *i.e.* from 22nd September, 1958 till 6th January, 1959 and, as shown in Table V, the ratio obtained over this three and a half month period was 150 : 16 : 1.

In the 18 catches in which detailed readings were made, interesting sets of figures were obtained. The writers are, however, rather at a loss to know how best to express the results. They are given here as arithmetic means for the flow per hour,

but it is felt that this may not be the most correct measure of the central tendency. The distribution of the figures is not geometric, nor do they form Poisson series. Certain other transformations were suggested as applicable by Mr. H. L. Manning, of the Empire Cotton Growing Corporation's Research Station at Namulonge, Uganda, but these cannot be used except at the 120-foot level because of the very large percentage of zero readings at other levels. It is hoped that future work with more sensitive instruments may overcome this difficulty.

TABLE III.—*Wind flow in decametres per hour, near ground level, in the canopy and above the canopy, Mpanga Forest. Eighteen periods of 24 hours each. Arithmetic means.*

	Level (feet)		
Time	6	60	120
06–07	0·2	1·4	125·1
07–08	0·1	4·4	247·2
08–09	1·1	24·6	355·8
09–10	3·6	48·8	381·7
10–11	2·4	97·7	486·3
11–12	7·7	119·0	577·5
12–13	16·8	180·8	723·1
13–14	14·8	160·5	762·3
14–15	9·5	182·1	897·1
15–16	12·2	133·6	803·6
16–17	4·1	80·8	730·4
17–18	0·2	27·4	489·0
18–19	—	0·4	114·9
19–20	—	1·3	112·3
20–21	—	3·8	129·9
21–22	<0·1	6·8	132·3
22–23	—	10·2	129·5
23–24	—	8·3	95·5
00–01	—	3·9	89.1
01–02	<0·1	6·1	92·7
02–03	—	2·3	126·9
03–04	—	1·9	137·6
04–05	—	4·8	103·9
05–06	—	0·9	154·2

The total flow in these 18 periods was :

120 feet	140,194		107 :
60 feet	19,867	or	15 :
6 feet	1,311		1

On weekly run of the wind for this whole period the results were :

120 feet	774,580		150 :
60 feet	82,331	or	16 :
6 feet	5,155		1

In the graph (fig. 6) an arithmetic scale has been used, as only thus can the great differences between day and night and between the various levels be adequately shown. From Table III and from this graph it is at once evident that daytime is the windy period. In fact, at ground level, recordable wind is almost confined to the afternoon. In the canopy the period is more prolonged, but at both these levels there is virtually no wind by night. Above the canopy the wind flow builds up hour by hour from sunrise to a clear maximum in mid-afternoon, after which there is an abrupt fall. By sunset the mean flow per hour has become very small and it remains so until after sunrise. Thus once more there is probably little if any barrier

to the upward diffusion of mosquitoes by night, though it is to be admitted that as yet nothing is known of the threshold values of flow which may inhibit such movements.

More detailed work, involving additional levels and the use of more sensitive instruments, is planned, as the differences in pattern and total flow here described have been by far the most striking results obtained during the present investigation.

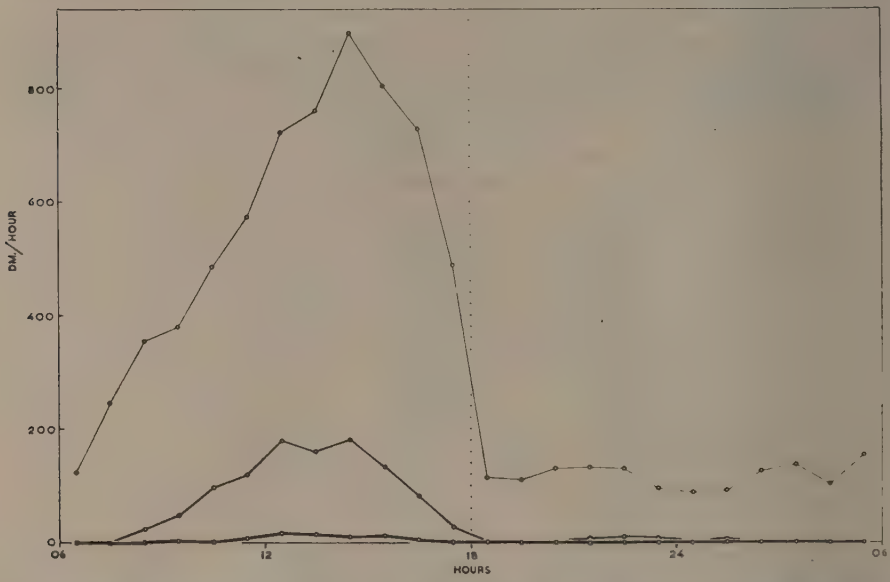

Fig. 6.—Mean wind flow in decametres per hour in eighteen 24-hour periods, by single hours. Thick line—ground level (6 feet); medium line—canopy (60 feet); thin line—above canopy (120 feet).

Light

In the case of vertical gradient Allee (1926) obtained the following ratios in the Barro Colorado Forest:

Emergent trees (125 feet or more)	442
Upper canopy (75–80 feet)	25
Lower trees (40–60 feet)	6
Small trees (20–30 feet)	3
Higher shrubs (10 feet)	1+
Forest floor	1

In the Semliki Forest, Haddow, Gillett and Highton (1947) obtained the following ratios:

Canopy (54 feet)	5
Understorey (31 feet)	3
Small trees (16 feet)	2
Forest floor	1

These figures are not unlike those for the last four levels in Allee's list, which correspond roughly in height, though relatively more light penetrates to ground level in the Semliki Forest. As in the case of wind, the great change occurs at the upper canopy limit. In the Mpanga forest, however (in the vicinity of the tower at least), the canopy is much less dense than in the two forests just mentioned. The figures

given by Dirmhirn (*see* Part III) show this rather well as, at Mpanga, the most marked change occurs at a relatively low level, between canopy and understorey. Her results may be compared with those given above as follows :

Highest emergent trees (120 feet or more)	12·5
Numerous emergent and partially emergent trees (90 feet) .	9·5
Mid-canopy (60 feet)	4·0
Understorey (30 feet)	1·5
Ground level	1·0

The conclusion is that at the tower site a good deal of light penetrates to ground level, the ratio being 4 : 1 only, as opposed to 5 : 1 and 6 : 1 for corresponding levels in the Semliki and Barro Colorado Forests.

With reference to daily trends, it is obvious that much more work will have to be done before any general conclusions can be drawn. Thus Evans (1939), working in Nigeria, found that the illumination in the Shasha Forest undergrowth rose fairly steadily till just after midday and thereafter declined. The work of Duke in the Cameroons (1955*a* and *b*) has shown varying patterns at different levels. Some of his graphs show a decrease in light intensity at ground level slightly before, or slightly after, noon and one of us (*A. J. H.*), working in Zika Forest near Entebbe and in the Semliki Forest in Western Uganda has found that near the forest floor light intensity sometimes shows a strongly biphasic pattern, with peaks in the morning and afternoon and a period of lower intensity around midday, when the crowns of the trees cut out much of the sunshine. The biphasic effect is naturally most pronounced where flat-topped trees such as *Piptadeniastrum* and *Albizzia* spp. prevail. It has an obvious bearing on mosquito biting-patterns, as these are similarly biphasic in many ground-haunting species (Kumm and Novis, 1938 ; Bates, 1944 ; Haddow, 1960).

Summary

1. Series of readings were made with the help of recording instruments in the Mpanga Forest, Uganda. The main environmental factors studied were temperature, saturation deficiency, wind direction and wind speed. These readings were made at 116–120 feet (above the canopy), 56–60 feet (in the canopy) and 6 feet ("ground level").

2. Where temperature and saturation deficiency were concerned, the differences between the canopy and the air above it were small at all times. During the day the readings at ground level were lower than those above, but the differences were much smaller than those recorded elsewhere by other workers. On the other hand, there were very striking differences at all levels between days on which rain fell in the afternoon and days when it did not. Differences between days were, in fact, more important than differences between levels. By night there was no significant difference between the levels, and there was therefore no microclimatic barrier to prevent the diffusion of mosquitoes from the forest into the atmosphere above it at this time.

3. The ratio of wind flow above the canopy to flow in the canopy to flow at ground level was approximately 150 : 16 : 1. At ground level recordable wind was virtually confined to the afternoon and even in the canopy there was very little wind by night. Above the canopy there was much wind by day, with a maximum in mid-afternoon. After sunset, however, there was very little flow even at this level, and once again it seemed to present little or no barrier to the upward diffusion of mosquitoes by night. The prevailing winds were south to south-westerly at all times of the day and night.

4. It is pointed out that at ground level in forest light intensity may be biphasic, with peaks in the morning and afternoon and a period of lesser intensity around midday. The biting cycle of many ground-haunting mosquitoes shows a similar pattern.

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

III. LIGHT INTENSITY AT DIFFERENT LEVELS

By Inge Dirmhirn

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The high tower on which these studies were carried out, and the forest in which it is situated, have been described in Part I of this series.

Radiation penetrating any plant cover is markedly changed. The change is essentially similar to that occurring at or in any sort of filter. Part of the radiation is directly reflected at the surface and part of that which has entered is scattered, and reflected back from inside the plant cover, augmenting that which has been directly reflected. The magnitude of the albedo, the sum of the directly and indirectly reflected radiation falling within the wavelengths of solar radiation (0·3–3·0μ), is very important in relation to all sorts of heat exchange in soil or in the plant cover in general, as it gives an index of that part of the radiation which has been absorbed by the soil or vegetation and transformed into heat.

Radiation which enters plant cover is partly reflected by the leaves and other parts of the plants, and partly absorbed by them. Thus only a certain (usually very small) fraction of the incoming radiation penetrates the plant cover and reaches the soil surface.

On its way through the foliage, radiation is changed in two different ways :

(1) in its intensity ;

(2) in its spectral characteristics.

With reference to (1) : part of the radiation is necessary to the plants for evaporation and to warm them and the ambient air. These aspects are not dependent on wavelength. Every " colour " (every wavelength) that is absorbed can be changed into heat.

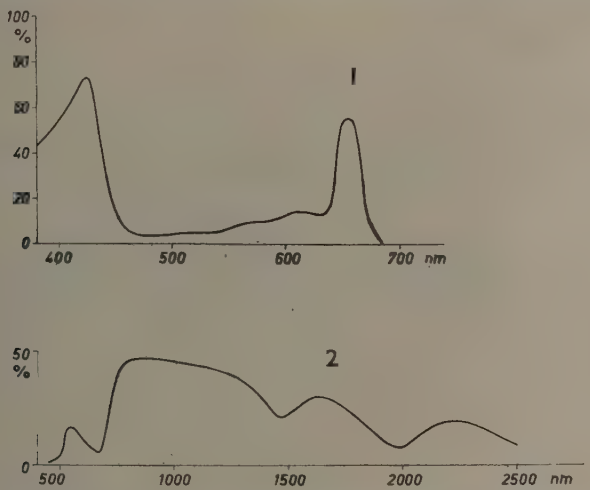
With reference to (2) : green plants require for photosynthesis certain wavelengths, particularly in the blue and red spectral range (fig. 1). It is obvious that, after penetrating a dense plant cover, radiation will show a lack of those colours. On the other hand, it has much green and, particularly, infra-red, in which range the maximum penetrating radiation is found (fig. 2).

When measurements are made with an instrument that is sensitive to all radiation from 0·3–3·0μ, penetrating radiation at the foot of plant cover will give higher readings than when an instrument sensitive to the visible parts of the spectrum only is employed, because the maximum transmission occurs in the infra-red wavelength. The visible parts of the range are, nevertheless, the most important for plants, man and animals, on account of their physiological significance where vision and photosynthesis are concerned.

Insects reach maximum visual sensitivity in the range of wavelengths visible to man, though they are able to see further into the shorter wave range (von Frisch, 1948). As our knowledge of the real spectral range of sensitivity of the insect eye is not adequate to permit adaptation of an instrument to cover this special case, one covering the spectral range and sensitivity of the human eye was used in this work to measure the intensity of light penetrating the forest. This instrument was a selenium photoelectric cell, corrected to human visual sensitivity by a Dresler filter. The photoelectric output was measured by means of a microammeter.

During August, 1959, measurements of incident, reflected and penetrating light were made on the steel tower in the Mpanga Forest Reserve. Two instruments were employed. One was set up on top of the tower to record incoming radiation, which of course altered with time (height of the sun) and sky conditions (amount and type of cloud). The second was used for measurement at different levels. As the measurements were made simultaneously, it was possible to find the proportion of penetrating to available light. It was thus possible to study the optical characteristics of the forest in the same manner in which such studies are made in water layers. The aim of this study was to determine the *percentage of available light penetrating to different levels above ground.* If the relative light intensity at different levels is once established, it becomes possible to deduce the absolute intensity at any given moment by using the results obtained at a nearby meteorological station where a record of daylight illumination is kept.

In a high forest such as Mpanga, there is only a small amount of reflection. The albedo of the forest in the neighbourhood of the tower, measured with a star-pyrano-



Figs. 1–2.—(1) The spectral absorption curve of chlorophyll *a* (after Rabinowitsch, 1951). (2) The spectral transmission curve of green plants (after Sauberer and Härtel, 1959). (*nm* = 1 mμ or 10Å)

meter, was only 9·4 per cent. on an average, and visual albedo, measured with a photoelectric cell, not more than 2·3 per cent. These are small figures when compared with the reflection from a meadow, which shows an albedo of 23 per cent., and 7 per cent. visual albedo. As the reflecting surface is the same in both cases (green plants), the small albedo of the forest, as compared with that of the meadow, is considered to be due to the high vertical distribution of the plants in the former, where they constitute a form of light trap. As the figure of 2·3 per cent., quoted above, is very small, it may be deduced that almost all light reaching the forest surface penetrates into the forest.

Figure 3 shows the decline in light intensity (percentage of available light) from the top of the tower to the bottom. The curve was worked out both for overcast and clear skies. When the sky is overcast radiation penetrating the plant cover is usually even greater than it is on days with clear sky. Clear skies and sunshine lead to the formation of many sun-flecks in the forest, with deep shade nearby, so that it is difficult to obtain fair average readings. The average intensity, however,

seems not to differ greatly whether the sky is clear or overcast, and in comparing the figures obtained in clear, as opposed to overcast weather, some workers have found them to be higher, while others, in different forests, have found the reverse (for reference, *see* Sauberer and Härtel, 1959). The average of the eight points measured on every platform of the Mpanga tower, however, showed but little difference between clear and cloudy weather (fig. 3).

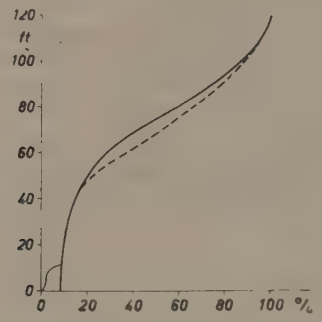


FIG. 3.—The vertical distribution of light intensity (percentage of available light) in Mpanga Forest. Unbroken line—average in overcast weather; broken line—average in clear weather; thin unbroken line—below undergrowth.

The decline of light intensity down to about 110 feet is slow, provided that crowns of trees are not directly above the point of observation. Below this the intensity decreases rapidly in the zone where the dense crowns of trees are close to the tower. The decline is slightly less in the tree-hole zone beneath. At the bottom a relatively high light intensity of about 8 per cent. was found. According to Germain and Evrard (1956) the average minimum light intensity in tropical forest is about 0·5 per cent. Such intensities were, indeed, found below the undergrowth in the immediate vicinity of the tower, the percentage being 0·3–0·5 per cent. of the total incident radiation at a distance of 10 feet from the tower. Thus the unexpectedly high readings just below the tower are attributed to the absence of undergrowth at this point.

The curve delineated in figure 3 shows the decline in average light intensity platform by platform. As the intensity was measured at different places at these levels, figure 4 and Table I are included, to show the distribution of light intensity at a distance of 6 feet from the edge of each platform. At each level three measurements were made from each side of the platform. The average was computed from

TABLE I.—*The light intensity (percentage of available light) as measured at three points each side of various platforms*

	Side											
	I			II			III			IV		
Point No.	1	2	3	4	5	6	7	8	9	10	11	12
110 feet .	96·0	95·0	97·0	95·0	94·0	94·0	97·0	94·0	94·0	95·0	93·0	94·0
90 feet .	17·0	31·0	59·0	86·0	83·0	84·0	88·0	86·0	87·0	88·0	85·0	81·0
60 feet .	26·5	31·5	34·5	42·5	43·0	43·0	15·5	14·5	17·0	17·5	24·5	21·5
30 feet .	22·5	24·0	27·5	29·5	27·0	26·5	15·0	13·0	14·0	16·0	16·5	18·0
20 feet .	12·5	17·3	16·0	7·7	6·7	10·1	10·7	2·5	9·4	14·6	14·2	16·4
Ground level .	5·3	4·6	4·6	5·0	9·1	5·3	9·0	10·2	10·5	14·7	11·8	10·7

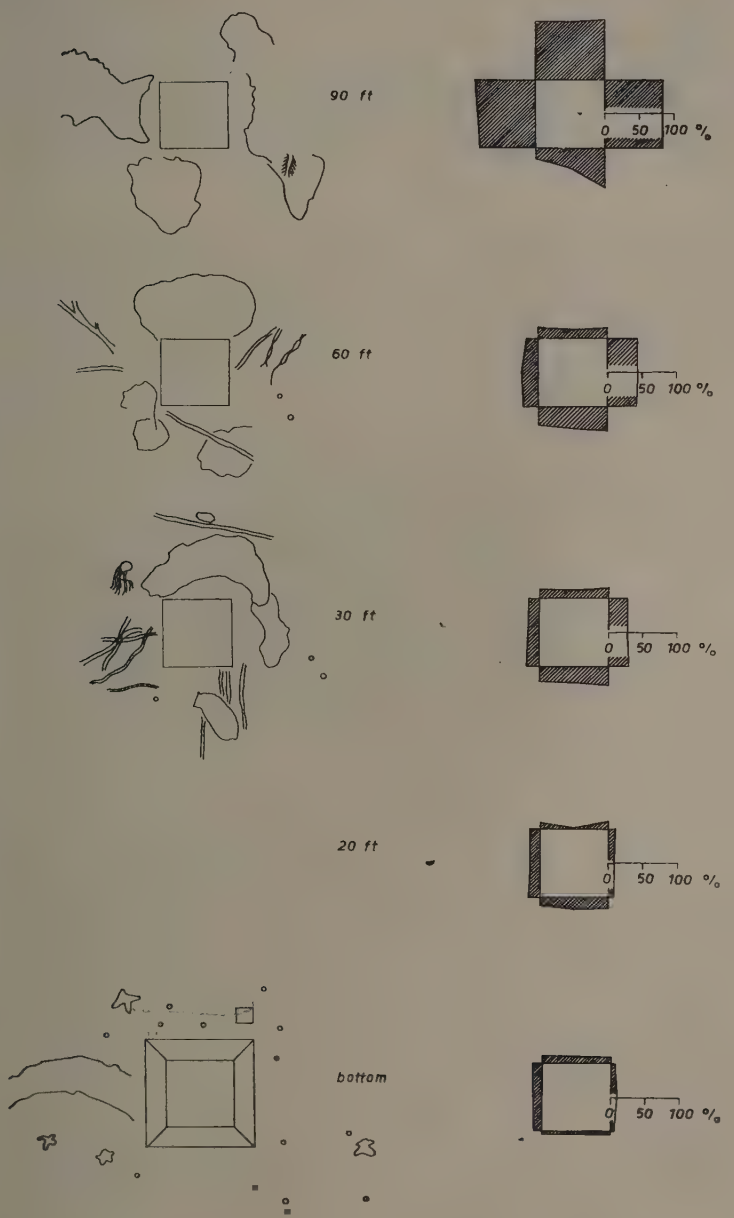


FIG. 4.—The light intensity on each side of the platforms and its relation to distribution of vegetation. At the 20-foot level no shading vegetation stood close to the tower.

six such series, made in overcast weather, and is given for each side of the platforms. This shows the influence of the trees immediately surrounding the tower, and demonstrates that the intensity at a given level may, if there is a mass of foliage close at hand, be less than that at a lower level where no such obstruction is present. In addition to the diagrams showing the light intensities at the different levels, the actual distribution of trees and foliage is shown. There is a clear inverse relationship between the light intensity and the density of the vegetation at the level considered.

Acknowledgments

The writer wishes to thank Drs. A. J. Haddow, J. D. Gillett and Philip S. Corbet, East African Virus Research Institute, for help during the work and for correcting the manuscript, and Mr. H. C. Dawkins, Forest Ecologist, Uganda Protectorate, for help in preparing the vegetation diagram in figure 4.

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

IV. MOSQUITO BREEDING AT DIFFERENT LEVELS IN AND ABOVE THE FOREST

By Philip S. Corbet

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Introduction

Between November 1957 and November 1959 mosquito breeding was studied in Mpanga Forest. A description of this habitat, and the full names of the species encountered, have been given in Part I of this series of papers ; here it need only be mentioned that the steel tower used for much of the work stood about 70 yards from the forest edge.

The aims of the work were to record the larvae occurring in natural sites in the forest near ground level, and to determine the vertical distribution of oviposition activity within and above the forest. Although the pressure of other commitments made it necessary to restrict the scope of both sections of the work, it is thought that the results, particularly those relating to vertical distribution, are sufficiently well-defined to merit presentation.

An initial survey of natural breeding sites was made in November 1957. About a year later, and after erection of the tower, the vertical distribution of oviposition activity was studied by using bamboo sections as artificial breeding sites.

The use of artificial breeding places to study choice of oviposition sites in wild mosquitoes was initiated by Buxton and Hopkins (1927) in Samoa, and by Dunn (1927*a*) in Nigeria. It was Dunn (1927*a*, *c*) who demonstrated the value of bamboo sections for the study of breeding in tree-holes and small-containers, and subsequently this method has been used with success by numerous workers, notably Shannon (1931*a*) in Brazil, and Philip (1933) in Nigeria. Although bamboo sections (" bamboos ") have usually been used at or near ground level, it happens that they are particularly suitable for studies of vertical distribution, since natural sites at higher levels are seldom accessible. In peri-urban areas in East Africa, bamboos have been used to reveal vertical breeding preferences in *Aedes simpsoni*, which favours a height of 60 feet (Harris, 1942), and *Ae. aegypti*, which oviposits more readily at ground level than above it (Harris, 1942 ; Teesdale, 1955). It is in forest, however, where ecological stratification can play an important role in disease transmission, that great significance attaches to the vertical distribution of mosquito breeding. Hingston (1932) was one of the earliest observers to record mosquitoes breeding at high levels in forest. Pittendrigh (1950*a*), in an intensive study of two species of *Anopheles* inhabiting bromeliads in Trinidad, demonstrated clearly that each oviposited at its own preferred level, which was correlated with the humidity requirement of the adult, and furthermore that this specialisation affected the geographical distribution of the two species, and therefore the incidence of malaria in the region. Other investigations in forest, involving the use of bamboos at different levels to study tree-hole breeding (Garnham, Harper and Highton, 1946 ; Galindo, Carpenter and Trapido, 1951 ; Laarman, 1958 ; Surtees, 1959) lead to the general conclusion that, whereas certain species exhibit a broad preference for a particular level, others breed indiscriminately from ground to canopy. Up to the present, such investigations have necessarily been restricted to levels within and below the canopy. It is, however, of interest to know whether the upper limit of the foliage presents an

ecoclimatic barrier to oviposition by mosquitoes in the canopy, and therefore at Mpanga observations were extended up to a height of 120 feet, well clear of the canopy and about 50 feet above it. It will be appropriate at this stage to mention the vertical ranges over which observations have been made by the other workers to whom reference will frequently be made, since such information provides a necessary qualification to any comparisons which can be drawn. Garnham *et al.* (1946) in the Kaimosi Forest, Kenya, placed bamboos at intervals of 10 feet up to 60 feet, about 20–30 feet below the top of the canopy. Laarman (1958) working near Irangi, Belgian Congo, extended observations up to about 75 feet (25 m.), where the height of the main canopy was about 90–120 feet. Surtees (1959), near Ilobi, Nigeria, placed bamboos " at intervals " up a tree 330 yards inside forest and heights at which collections were made apparently included ground level, 25 feet and 50 feet.

Methods

At Mpanga, bamboos were placed at 13 levels on the tower, from ground level to 120 feet, at vertical intervals of 10 feet. They were each about 12–15 inches high and had a diameter of 3–4 inches. They were attached to the inside of the corner buttresses at each level, and were therefore in the least exposed positions possible on the tower. Even so, at 120 feet they were often cracked by the sun. Bamboos that were transferred to a different level were first immersed in near-boiling water to kill any persistent eggs or larvae.

A second series of bamboos was attached to trees around the tower, at various heights from ground level to 12 feet. These provided a control for the two lowest sets on the tower itself. Fifteen collections were made, at intervals of approximately three weeks. On each occasion larvae were identified and pupae allowed to emerge. A record was kept of the species present, but not of the numbers of larvae, since the purpose of the investigation was to determine the frequency of visits made by ovipositing females to different levels.

Results

Natural sites

At the time of the initial survey, in November 1957, the water table was unusually high, and ground pools were numerous. Tree-holes, however, are scarce at Mpanga. Dunn (1927*b*) found that in West Africa most tree-holes suitable for mosquito breeding were caused by human damage, or by the decay which ensued, and the scarcity of tree-holes in Mpanga is probably related to the fact that it is a Forest Reserve where cutting and felling are restricted. In this connection it is interesting to note that Laarman (1958) encountered a marked scarcity of suitable tree-holes, and

Table I.—*Species found breeding in natural sites*

Species	Ground pools	*Dracaena* axils	Tree-holes
Toxorhynchites brevipalpis	—	—	+
Anopheles implexus	+	—	—
Uranotaenia nigromaculata	+	—	—
Aedes apicoargenteus	—	—	—
Ae. africanus	—	—	+
Ae. mutilus	+	—	—
Ae. phyllolabis	+	—	—
Ae. palpalis	+	—	
Eretmapodites hightoni	—	+	
Culex nebulosus	—	+	—
C. semibrunneus	+	—	—
C. trifoliatus	+	—	—

concluded that this might represent a factor limiting the breeding of certain sylvan mosquitoes. In this instance, however, the limit was apparently imposed, not by a scarcity of cavities, but by their inability to retain water.

Mosquitoes found as larvae or pupae in natural sites at Mpanga are listed in Table I.

In ground pools, which were heavily shaded and contained much leaf litter, the commonest species was *Aedes mutilus*. In *Dracaena* axils, which were usually from 3–5 feet above the ground, *Culex nebulosus* was commoner than *Eretmapodites hightoni*, the identity of which was established by rearing out male adults. In tree-holes the commonest species was *Ae. africanus*.

TABLE II.—*Numbers of occurrences at different levels*

Species	Control series (0–12 feet)	Tower series (height in feet) 0	10	20	30	40	50	60	70	80	90	100	110	120	Totals for tower series
Toxorhynchites brevipalpis	21	5	4	4	2	4	2	3	3	2	1	2	.	.	32
Aedes longipalpis	5	.	2	2	1	.	.	3	.	.	.	.	.	.	8
Ae. apicoargenteus	6	1	1	2	5	6	6	9	9	10	12	11	12	7	91
Ae. dendrophilus	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Ae. africanus	18	1	1	.	1	1	.	1	.	.	.	.	1	.	6
Ae. capensis group	.	.	.	1	.	.	.	1	.	1	.	1	.	.	4
Eretmapodites semisimplicipes	38	11	7	10	9	7	11	9	5	6	5	.	.	.	80
E. oedipodius group	3	2	1	.	2	.	.	.	.	.	.	.	.	.	5
Culex albiventris group	10	.	.	1	.	1	.	.	.	.	.	.	.	.	2
C. nebulosus	11	2	2	2	4	4	2	5	4	4	4	3	4	.	40
C. cinerellus	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
C. macfiei	8	2	4	2	.	1	1	1	.	.	.	.	.	.	11
Culex sp. indet.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
Number of collections	57	13	13	14	13	13	14	14	13	14	15	13	12	7	168
							Limits of canopy								

Vertical distribution in bamboos

Table II records the number of times the species collected were found at different levels. In this table, the " number of collections " comprised only those from bamboos which contained mosquito larvae, since the incidence of fouled or empty bamboos was not the same at all levels owing to differential exposure to the sun.

Collections consisted mainly of four species (*T. brevipalpis*, *Ae. apicoargenteus*, *E. semisimplicipes* and *C. nebulosus*), three of which show a non-random vertical distribution. For these species, at any rate, it can be assumed that bamboos near ground level on the tower provided a good index of breeding at corresponding levels in the forest nearby, since percentage occurrences (*i.e.* occurrences as a percentage of collections) below 12 feet on, and near, the tower were almost identical. They were, respectively: *T. brevipalpis* 35 and 37 per cent.; *Ae. apicoargenteus* 8 and 11 per cent.; and *E. semisimplicipes* 69 and 67 per cent. Of the other species, only *Ae. africanus* appeared to be significantly rarer in the tower bamboos than in those nearby, an observation which is discussed in the annotated species list which follows.

Toxorhynchites brevipalpis conradti

This species breeds mainly within the forest, from the ground to just above the canopy, being found in only 6 per cent. of collections above 90 feet, and in none above 100 feet. Ground level is favoured most, and the region above the canopy

least (Table III), but further analysis shows that from 20 to 70 feet breeding is evenly distributed. It thus seems to breed lower in Mpanga than in Kaimosi, where it was found to favour heights of 50 feet and over (Garnham *et al.*, 1946). *T. brevipalpis* is evidently more restricted to forest vertically than it is horizontally at ground level. Although a common sylvan mosquito in Bwamba, it may occasionally breed there in open ground and plantations (Haddow *et al.*, 1951), whereas elsewhere in Uganda and in Nigeria it may breed in scrub outside forest and also in villages (A. J. Haddow and J. D. Gillett, *personal communication*; Surtees, 1959). At Mpanga it has been recorded from a tree-hole in a forest clearing. As an obligate predator, this species is said usually to be the sole occupant of a small breeding site (Hopkins, 1952), and it was never found by Surtees (1959) in company with *E. chrysogaster*. Of the 53 occasions when it was encountered at Mpanga, however, it was alone on only 21 per cent., and together with *E. semisimplicipes* on at least 36 per cent.

Aedes longipalpis

At Mpanga this species occurred up to 60 feet. Garnham *et al.* (1946) found it more often in tree-holes at 18 feet than at ground level, and considered that it bred more at higher levels.

TABLE III.—*Percentage occurrence of four species*

Species	Type of pot	Height range in feet			Significance of inter-level differences	
		0–30	40–70	80–110	X^2	P
Toxorhynchites brevipalpis	All	28	22	10	5·901	<0·02
Eretmapodites semisimplicipes	,,	70	58	21	27·102	<0·01
Aedes apicoargenteus	,,	17	56	83	42·872	<0·01
Ae. apicoargenteus	Predator-free	11	54	90	24·521	<0·01
Culex nebulosus	All	19	24	29	1·523	>0·1
C. nebulosus	Predator-free	56	38	28	2·743	*ca.* 0·1

Ae. apicoargenteus

Breeding was most frequent above 100 feet and progressively declined below this. The vertical distribution was strikingly regular (fig. 1), and is of particular interest since the trend shows no apparent interruption at the top of the canopy. These results confirm and amplify those of Laarman (1958) and Surtees (1959), who both found this species to feature most frequently in the highest collections. For a sylvan mosquito, *Ae. apicoargenteus* evidently has a wide ecoclimatic tolerance. In Tanganyika, it will breed in open rock-pools on the lake shore or even in domestic containers (Harris, 1942); in Nigeria it was found to show a preference for scrub over forest (Surtees, 1959); while in the Belgian Congo, Laarman (1958) found that, of four sylvan species, *Ae. apicoargenteus* was the only one which bred equally in both dense forest and clearings. The latter observation led him to suggest that a response to light might determine its vertical distribution. This seems very likely, since it has recently been found that *Ae. apicoargenteus* oviposits most frequently near midday (Haddow, Corbet and Gillett, 1960), a time when light-gradients are well-defined, but when, on the contrary, the microclimatic "barrier" provided by the canopy is most severe (Part II). In this connection it may be noted that Surtees (1959) correlated leaf-fall with a seasonal rise in the incidence of *Ae. apicoargenteus*, and suggested that this might result from the contamination of sites with decaying vegetable matter. The observations recorded above, however, indicate the additional possibility that leaf-fall would favour breeding of this species by increasing the number of unshaded sites in forest.

Ae. dendrophilus

Larvae were found occasionally at ground level and on the tower at 30, 70 and 100 feet, though not in the series of bamboos recorded in Table II.

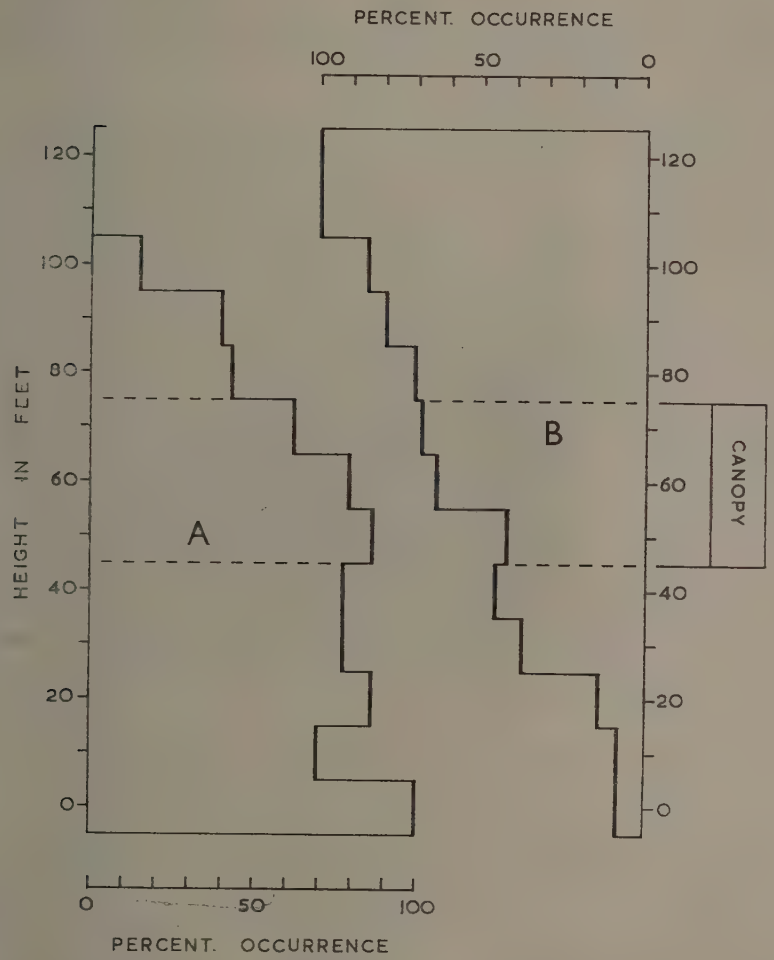

Fig. 1.—The complementary vertical distribution of certain mosquitoes at Mpanga. *A*, the predators, *Toxorhynchites brevipalpis* and *Eretmapodites semisimplicipes*; *B*, *Aedes apicoargenteus*.

Ae. africanus

Larvae occurred occasionally up to 110 feet, but frequently at ground level. In Kaimosi, also, this species bred mainly at ground level, although being found occasionally up to 50 feet (Garnham *et al.*, 1946). Laarman (1958) found it to have a similar distribution in the Congo. These observations are consistent with the marked preference it shows for heavily shaded forest tree-holes (Laarman, 1958), which may indicate why, at Mpanga, *Ae. africanus* was the only species for which ground level

collections on, and near, the tower differed significantly, since the base of the tower was necessarily less heavily shaded than sites nearby (*see* Part III. p. 272).

Ae. capensis group

Larvae may have included *Ae. capensis* and *Ae. haworthi*, both of which were collected as adult males in light-traps on the tower. At Mpanga, larvae occurred up to 100 feet and, in Kaimosi, larvae of *Ae. capensis* were recorded from 60 feet (Garnham *et al.*, 1946).

Eretmapodites semisimplicipes

Males were reared from larvae collected at all levels (except 60 feet) up to and including 80 feet, and all were this species. All larvae of the *chrysogaster* group have accordingly been assigned to *E. semisimplicipes*, since no other species in the group was found at Mpanga during the present work. Larvae were extremely common at ground level and up to 60 feet, but their incidence declined rapidly within the canopy, and they were never found above 90 feet. This pattern of vertical distribution contrasts strongly with that observed by Garnham *et al.* (1946) in Kaimosi where, though common in shaded ground-level sites, this species was never found above 20 feet. In this connection it should be recorded that Haddow (Part VII, p. 316) took two female adults of the *chrysogaster* group (assigned to *E. semisimplicipes* on appearance, and confirmed by associated males) in biting catches in Mpanga at 30 feet, before any bamboos were placed on the tower. As long series of biting catches in Bwamba and Entebbe failed to reveal appreciable activity of the *chrysogaster* group above ground level (Haddow, 1956*b*), it may be that both the biting and oviposition behaviour of *E. semisimplicipes* are unusual at Mpanga. Contrasting results have, however, also been obtained for *E. chrysogaster*, which Laarman (1958) found to breed mainly below about 18 feet in the Belgian Congo, and which Surtees (1959) in Southern Nigeria recorded in undiminished numbers up to 50 feet. Larvae of *E. semisimplicipes* were very numerous at Mpanga, and predominated in collections up to 50 feet (Table II). As this species is known to be predatory (Haddow, 1946), it must have a considerable effect on the numbers of other small-container breeders below the canopy at Mpanga.

E. oedipodius group

Larvae occurred sparsely up to 30 feet.

Culex nebulosus

The ubiquitous breeding habits of this species are well known (*see* Hopkins, 1952). At Kaimosi, Garnham *et al.* (1946) found it to be most abundant at 40 feet, although occurring up to 60 feet; Surtees (1959) records it as breeding mainly at 25 feet. At Mpanga it occurred from ground level to 110 feet, being found at more levels than any other species except *Ae. apicoargenteus*. Grouped records (Table III) reveal no significant preference for level, but numbers are too small to rule out the possibility that one may exist, although it can hardly be well marked. As noted previously by Lumsden (1955), newly-filled bamboos are particularly attractive to this species. At Mpanga the number of such bamboos offered was the same at all levels.

C. cinerellus

One larva was found at 50 feet.

C. macfiei

Larvae were not uncommon at ground level and up to 20 feet, and they occurred sparsely up to 60 feet.

Culex spp.

These included two larvae of the *Culex* (*Neoculex*) *albiventris* Edwards group, from 20 and 40 feet.

Discussion

Within and below the canopy at Mpanga, the overall picture of small-container breeding is one of intense predation. *E. semisimplicipes* and *T. brevipalpis* are principally responsible for this, and both are commonest at ground level and least frequent in the canopy. On the tower, one or both of these predators occurred in every collection at ground level, and in progressively fewer at higher levels, until their limit was reached just above the canopy.

It is clear that the presence of these two species must affect the numbers of other mosquitoes, especially *Stegomyia* spp. It has been shown by Shannon (1931*a*) that *Stegomyia* larvae are, on account of their characteristic restlessness, exceptionally vulnerable to certain predators (including *Toxorhynchites*), and that their numbers are inversely proportional to those of the predators present. Haddow (1948), in a study of mosquitoes breeding in plant axils, attributed differences in the densities of larval *Stegomyia* and *Uranotaenia* spp. to the activities of *Eretmapodites*. This being so, it might readily be supposed that the pattern of vertical distribution recorded for *Ae. apicoargenteus* owes its form to the preference predators show for breeding at lower levels, since the respective distributions of predator and prey are almost complementary (fig. 1). It is obviously important to be able to distinguish between this possibility and the alternative one that *Ae. apicoargenteus* may exhibit a real preference for breeding at higher levels.

To obtain information on this point, at each site, beside the normal bamboos, were placed others that had been modified with the view of excluding predators. The modifications were similar to those used by Galindo (1958) for experiments with *Sabethes* : the top was covered and a single hole (of diameter three-quarters of an inch or one and a half inches) was bored in the side near the top. The bamboos with the smaller hole excluded most *T. brevipalpis*, but *E. semisimplicipes* continued to breed in all types of bamboo in undiminished numbers ; thus this approach did not prove successful.

It is, however, possible to obtain the same information in another way, providing predators are not found in all containers. For instance, if it be supposed that the observed distribution of *Ae. apicoargenteus* is determined not by preference for level but by predation alone, then the occurrence of this species in " predator-free " bamboos should be independent of level. (" Predator-free " bamboos may be defined as those which contain mosquito larvae but not predators.) Analysis reveals that the trend observed in predator-free bamboos is indistinguishable from that found in all bamboos (Table III), and furthermore that in this series the differences recorded between levels are highly significant in each case. Accordingly it must be assumed that, at Mpanga, *Ae. apicoargenteus* shows an increasing preference for higher sites, to the extent indicated by the data, and that although its vertical distribution may be affected by predators, it does not appear to be determined by them. It seems that *Ae. apicoargenteus* is well adapted for existence in forest habitats where there is heavy predation by either *Eretmapodites* or *Toxorhynchites*, or both, since it oviposits least where predation is greatest. Furthermore, in the event of scarcity of tree-holes becoming a limiting factor in the canopy or in crowns of emergent trees, it can breed successfully at ground level outside forest, where such predation is less severe. By the same token, the breeding habits of *Ae. africanus* would seem to make it very susceptible to predation, since it prefers heavily-shaded sites and is concentrated at ground level.

These considerations show that it is important to make allowance for the presence

of predators when the breeding preferences of the prey are being determined. Such allowance should in fact be made in all cases where predators show a non-random distribution, and this will of course necessitate attention being paid to predators other than mosquitoes as well. It seems that, in future studies of this kind, use should be made of what may be termed the Predator-free Index, namely the percentage occurrence in sites containing mosquito larvae but no known predators.

If data are analysed in this way it should be possible to estimate the effect of predation, by comparing the frequency of occurrence of a prey species in sites with and without predators, respectively. An unexpected feature of the present results for *Ae. apicoargenteus* is that these two categories do not differ significantly, despite the obvious fact that predatory mosquitoes were very active. Slight differences are revealed by comparing these two values in the case of *C. nebulosus*, but they could be due to random agencies (Table III). To throw further light on this question it may be necessary to record the number of larvae, as well as the species present in each site.

Other Inhabitants of Small Containers

The fauna of tree-holes and bamboos at Mpanga was not studied in detail, but included two other animals which probably affected both larvae and adults of mosquitoes there.

Larvae of a dragonfly (Libellulidae: *Hadrothemis camarensis* Karsch) were found in 3 per cent. of 103 bamboos at ground level, and also occasionally at 10, 20 and 30 feet. These fed heavily on *Stegomyia* larvae in captivity and must be presumed to contribute to predation in forest at lower levels. Young (1921) and Shannon (1931*a*) have noted that dragonfly larvae prey heavily and selectively on *Stegomyia* larvae in captivity. It is possible, however, that the dragonfly larvae at Mpanga may represent a local faunal feature since, despite the extensive studies which have been undertaken by other workers using bamboo sections, there is apparently no previous record of African dragonflies having been found either in these or in tree-holes. Mellanby (1956) noted that dragonfly larvae occurred in earthenware pots at Ibadan, but the mouths of these pots had a diameter of 10 inches. At Mpanga, the internal diameter of the bamboo sections was usually less than 3 inches, and it was a common experience to find the remains of adult dragonflies in bamboos. These were invariably mature females and had presumably been unable to rise from the bamboo after oviposition.

Multi-scaled Forest Lizards (Lacertidae: *Algyroides africanus* Boulenger) were found in 2 per cent. of 103 bamboos at ground level, and also in tree-holes there, always being encountered singly. This species is known from several other forests in Uganda, where it basks in sunlight " beside some knot-hole or piece of loose bark ", in, or beneath which it can " seek refuge when disturbed " (Loveridge, 1942: 337). At Mpanga, it was observed that a lizard which had been disturbed would remain submerged for at least 30 seconds, if there was water in the cavity or bamboo. It was therefore considered likely that some feeding might be occurring beneath the surface, and stomachs of four specimens were examined to see if they had been feeding on mosquito larvae. However, the first of these, taken from a tree-hole containing numerous larvae and pupae of *Ae. africanus*, had eaten only a cockroach and a terrestrial beetle. Stomachs of the three others contained a cockroach, an isopod, a spider and a small gastropod. Loveridge (1942) recorded similar food and concluded that prey was taken from the ground. It is possible, however, that food may also be obtained inside cavities, from their walls above water-level, and that it may therefore include ovipositing or emerging mosquitoes.

Acknowledgments

I wish to thank Dr. A. J. Haddow for helpful discussions, and Mr. Y. Senkubuge for his careful assistance in the field. I am also grateful to Mrs. E. C. C. van Someren, who assisted with the identification of certain mosquito larvae, and to Miss A. G. C. Grandison, British Museum (Natural History), who identified the *Algyroides*.

Summary

1. Mosquito breeding in natural sites and bamboo sections was studied in Mpanga Forest. Observations extended from the ground to a height of 120 feet, about 50 feet above the canopy.

2. Several species exhibited a non-random vertical distribution of larval occurrence. *Toxorhynchites brevipalpis*, *Aedes africanus* and *Eretmapodites semisimplicipes* were commonest at ground level, and *Aedes apicoargenteus* above the canopy.

3. Predatory mosquitoes predominated below the canopy, particularly at ground level, where they are presumed to have affected the numbers of *Ae. africanus*. The observed vertical distribution of *Ae. apicoargenteus*, however, is shown to have resulted from a site preference and not from predation. It is stressed that these two factors should be clearly distinguished in future studies of mosquito breeding where predators are involved.

4. Results are discussed and compared with those of other workers. Two other insectivorous inhabitants of forest tree-holes are briefly mentioned.

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

V. SWARMING ACTIVITY ABOVE THE FOREST

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The high tower on which this work was carried out and the forest in which it is situated have been described in the introductory paper of this series (Part I) while the forest microclimate has been discussed in another (Part II).

Swarming activity in Diptera and other winged insects occurs typically around the sunset and sunrise periods, though in *Culicoides* it may begin in the afternoon (Parker, 1949) and in East Africa some Chaoboridae usually swarm in full daylight. The writers have seen large swarms of unidentified Stratiomyidae in mid-afternoon at Mpanga, but apart from these all the swarms observed occurred in the hour after sunset or in that before sunrise. In our work the clock is so adjusted that 1800 hours corresponds to the precise time of sunset (Part I, p. 253).

As swarming is a conspicuous activity, and as evening swarms occur at a time when many people are at leisure and walking abroad, it attracts a good deal of attention, and has been commented on by most of the classic writers on entomology from Ray (1710) onward; nor should Keats' excellent description of a swarm in his " Ode to Autumn " be forgotten; seldom has the whole character of swarming flight been so well described in so few words. Within the last 30 years it has received a great deal of attention from numerous workers in different parts of the world, but no general agreement on its function has yet been reached. There are, broadly speaking, two schools of thought, the one maintaining that it is an essentially sexual activity, and the other holding that, while swarming may have been sexual in the past it is now merely a vestigial or ritual behaviour, any connection it may have with mating being purely incidental. Such being the case it is necessary, before proceeding to a discussion of the Mpanga results, to consider some of the points that have been well established, and some that have remained controversial. The literature being voluminous, only a few papers can be quoted in the present brief review.

Swarms are commonly formed by males, though female swarms have been noted, for example in Empididae (Frohne, 1959), Ceratopogonidae (Downes, 1958) and mosquitoes (Nielsen and Nielsen, 1953). Most of the swarms described in the literature have been monospecific, but mixed mosquito swarms have been recorded by Rao, Roy and Rao (1942), Senior White, Lewis and Lee (1953) and Provost (1958), and mixed swarms of mosquitoes and Chironomidae by Nielsen and Greve (1950). In the present work the swarms almost invariably consisted of more than one mosquito species; Ephemeroptera and various families of Diptera, notably Tipulidae, Chironomidae and Stratiomyidae, were also well represented. Most of the material, apart from the mosquitoes and tabanids (which the writers retained), was passed to the late Dr. W. E. Snow for study, and it is feared, as a result of his sudden and tragic death, it is unlikely that it will ever be analysed and written up.

Swarms form in relation to a marker which, may be a major outstanding feature such as a tree or shrub in the case of mosquitoes (Nielsen and Greve, 1950; Nielsen and Nielsen, 1958) or a minor outstanding feature such as a bracken frond in the case of a small insect such as *Culicoides pallidicornis* (Downes, 1955). The swarm marker often consists of a patch darker than the background, as in *Culicoides*

nubeculosus (Downes, 1950). On the other hand it may be a patch paler than the background as in *Anopheles superpictus* (Nielsen and Nielsen, 1953). *Anopheles labranchiae* subsp. *atroparvus* can easily be induced to swarm over a white marker, and in such cases adjusts the size of the swarm, within limits, to that of the marker (Cambournac and Hill, 1940). Swarming under a marker has also occasionally been noted, for example by Hackett and Bates (1936) in captive mosquitoes, and by Hayes (1958) in *Culiseta melanura* in nature. Finally, in the case of *Anopheles philippinensis*, *A. vagus* and *A. kochi*, Wharton (1953) was unable to find any visible swarm markers.

The term " swarm " is a poor one as the dancing flight characteristic of swarming can be induced, by the presence of a marker, in a single midge (Downes, 1950) or mosquito (Rao and Russell, 1942; Nielsen and Nielsen, 1958). Each insect thus responds individually to the marker and the swarm builds up in relation to this stimulus only and not in relation to the presence of other insects. Most writers agree that swarming is reduced or inhibited by strong wind, but is favoured by slow air currents, each insect facing the wind and maintaining its position relative to the marker by its characteristic swarming flight (Rao and Russell, 1938; Cambournac and Hill, 1940; Downes, 1950), and Wharton (1953) has further noted that on entirely windless evenings males of *A. philippinensis* show no orientation in the swarms. Exceptions occur in the case of *Anopheles culicifacies*, and *A. aquasalis*, where the swarms face away from the sunset (Rao and Russell, 1942; Senior White *et al.*, 1953). A very interesting point has been brought out by Downes (1955) who has shown that " movement vision " plays a part in inducing the characteristic swarming flight as, to an insect drifting backward in a current of air, the marker must appear to be receding forward and a short compensatory flight is induced to restore the position. Limiting wind speeds are apparently those where this position can no longer be maintained. The well-known experimental work of Kennedy (1940) leads to a similar conclusion.

Numerous workers have shown that swarms form in the same place nightly and Bates (1941) has demonstrated that, in a large cage, swarm positions remained constant for a given species for 2 years. Nielsen and Nielsen (1953) have shown by marking experiments that in *Aedes taeniorhynchus* the same individual males swarm in one spot evening after evening, there being little exchange between swarms even when they are close together. On the other hand, Wharton (1953) noted that in *A. philippinensis* free exchange of insects might occur between swarms forming in close proximity to each other, and that such swarms might subsequently coalesce. Mosquitoes may enter and leave the swarms, and the stay of an individual in the swarm may be as little as one and a half minutes; further, males may drop out of a swarm to rest and subsequently rejoin it (Nielsen and Nielsen, 1953).

Other limiting factors in swarming appear to be temperature and light, humidity being unimportant. Different insects, however, respond in different ways. In this connection the work of Nielsen and Greve (1950) and Nielsen and Nielsen (1958) is of particular interest. These workers have followed the course of events in considerable detail and their observations are worthy of close study. In *Aedes cantans* small, very temporary " provoked swarms " may be formed by passage of an observer through an area where males are abundant, but spontaneous swarming does not begin till about an hour before sunset. The swarms formed at this time are free " ground swarms " at low level and not associated with a marker. Toward sunset " the ascent " occurs, and the mosquitoes form " top swarms " over trees, etc. Enormous " ceiling swarms " occur rarely. Unfavourable temperatures may delay the onset of swarming, which appears to begin in response to a certain rate of change in light intensity and to end at a certain light threshold value, in this case about 7 lux. In the morning the process is reversed. The importance of temperature is in determining the onset of evening swarming and the dispersal of swarms in the morning. This work may explain why other workers (such as Cambournac and Hill,

1940) have found such widely varying light intensities at the time of swarm formation. In other species the Nielsens found the response to be different. Thus in *Culex univittatus* both the beginning and end of swarming correspond to a certain threshold light intensity, while in *A. superpictus* both beginning and end correspond to a certain rate of change in light intensity.

So far this discussion has dealt with points which are fairly well established. Where the function of swarms is concerned, however, there is no unanimity. Almost every worker has noted the presence of females in the swarms and many have recorded copulation in them. On the other hand, many writers have pointed out that the number of females in swarms seems trivial in relation to the numbers known to be present in the area Cambournac and Hill (1940) were able to observe copulation occurring freely on walls, etc., in *A. labranchiae atroparvus*, but females were extremely rare in swarms and they conclude " . . . it is suggested that swarming has largely lost its influence on mating, though its ritual character is preserved ". Nielsen and Greve (1950) have pointed out that in *Ae. cantans* the small number of matings observed in swarms during a very extended study (three matings among millions of insects observed) has indicated unequivocally that mating in swarms cannot account for more than a minute fraction of what must be taking place in the area. Bates (1941) has pointed out that in the laboratory females seem entirely indifferent to the presence of swarms only a few centimetres away. Provost (1958) has noted that in certain *Psorophora* spp. there are special mating flights which are not associated with swarming. Further, in a case where a single brood was recognisable, male swarms formed on the second day after emergence, and were still being formed a fortnight later, though mating in this brood was long since over. In *Ae. taeniorhynchus* broods are easily recognisable (Provost, 1952 ; Nielsen and Nielsen, 1953). The females disperse widely, four days after emergence. The males remain near the point of emergence and swarm nightly. The crucial point is that the females must mate before dispersal, and this occurs before the males begin to swarm, which seems, in this species, to be about four days after emergence. No mating in swarms of *Ae. taeniorhynchus* has ever been seen by these workers.

Observers holding the opposite views are equally emphatic, and have produced some convincing evidence. Roth (1948) has established that mating responses in male *Aedes aegypti* depend upon antennal stimulation by certain sound frequencies, and that the response ultimately depends upon vibration of the erected fibrillae, this being mechanically transmitted to Johnston's organ by the antennal flagellum. In other words, recognition of the female depends on the presence of erect fibrillae. Now, while in *Ae. aegypti* the fibrillae, once erected, remain so for life (and the males will mate at any time), in other species they may be folded except when the male is in flight. This has been noted by Nielsen and Nielsen (1958) who, while not in general favouring the view that swarms are primarily sexual, noted that in *Aedes caspius* increasing numbers of males extended the fibrillae as sunset approached, and state " since mating is initiated only in flight, both Roth's experiments and our observations demonstrate that extended fibrillae in the male mosquito indicate readiness for flight. Roth showed clearly that fibrillar extension is necessary for a male to become attracted to the flight tone of the female, but the ability to hear may also be important for other flight activities, especially swarming ". If the point of view put forward by Downes (1958) be accepted, namely, that swarming depends on an individual visual response, then the suggestion that auditory responses play a part in the formation of male swarms should clearly be disregarded. The Nielsens themselves in the paper just quoted state that single mosquitoes may " swarm " and that the term " swarming " is unfortunate as " . . . it gives the impression of some kind of mass behaviour, implying that there is a certain amount of rapport between the individuals, a certain degree of gregariousness. This may be the case but there is no supporting evidence whatsoever . . . ".

There have been several records of direct observation of active mating in swarms. Rao and Russell (1942) observed " brisk " mating in the swarms of *A. culicifacies* which they studied and also (1938) observed mating occurring regularly in the nightly swarms of *Anopheles stephensi* in a cage. Wesenberg-Lund (1920) has described the direct, apparently purposeful flight of females of *Anopheles claviger* and of *Aedes communis* into the male swarm " which is then in a moment altered into a ball in which single individuals are pressed against each other ; in a few moments a pair drops out of the swarm and falls down into the grass where the mating is accomplished ". Hearle (1929) has described how, in a swarm of *Aedes flavescens* " the males danced slowly but whirled madly around when females approached and entered the swarm. Several matings were observed . . . [on a single evening] ".

It is, however, from other groups that the most critical evidence comes. It has been pointed out (Downes, 1958 ; Peterson and Wolfe, 1958) that there are two major groups in the Simuliidae. In one group the eye is sharply divided into facets of two sizes, one of which may be involved in close-range recognition, as the antennal recognition response is probably not adequate for specific distinction of the female by the male. Swarming and swarm pairing occur in this group. In the other, rarer, group swarming does not occur, and mating is brought about by other means. *Cnephia* sp., for example, meets the females while running randomly on mud surfaces. Much the same is the case in Ceratopogonidae. In *Atrichopogon* a pollen meal replaces the blood meal and here the males (which have reduced antennae) meet the females on flowers. In *Culicoides utahensis* the male meets the female in the ears of jack rabbits. The male sense organs in this species are almost entirely female in type, and they enable the male to find a warm-blooded animal, but not to find the female by means of the usual auditory response. Downes (1955) concludes that in those species of *Culicoides* which swarm the females respond to the male swarm marker and fly into the swarm, mating very rapidly after entry. In *Ceratopogon* the females may swarm just behind the males. Swarming is thus, he considers, a useful means of bringing dispersed males and females into proximity, after which auditory recognition of the females occurs. In an empid (*Rhamphomyia* sp.), female swarms form, and here the males fly into the female swarms to pair (Frohne, 1959).

The crucial question appears to be why males always seem to outnumber females so greatly in swarms. This may be answered at least in part by the observations of Gibson (1942) on *Spaniotoma minima* Meigen, a member of the Chironomidae. Here males and females swarm over the same marker, but males soon predominate as, after copulation has been completed by the pairs that have fallen from the swarm, the males rejoin it, while the females do not. Gibson found that in the laboratory the swarm at first contained a high proportion of females, but, by the process just described, the percentage of males soon rose to 93 per cent., about the level usually found in nature. This is also the case in mosquitoes, as Gillett (1955) has shown that male *Ae. aegypti* will copulate with as many as 8 females in quick succession, though only the first three or four of these are successfully fertilised. Further, he has found that in most cases the females, even in small cages, will not accept the male for some hours after the first pairing (*personal communication*).

Finally, an important and much neglected paper by Shannon (1931*b*) must be mentioned. Here it is pointed out that in South America swarming occurs typically among mosquitoes which are drab in colour or which at least do not give striking recognition patterns. Most of these are ground-water breeders, and are essentially nocturnal. Day-flying mosquitoes of the forest are often brilliantly coloured, as in *Haemagogus* and *Toxorhynchites*, or they may have striking adornments and characteristic behaviour, as in *Limatus* and the sabethines. Many of these species, Shannon points out, are small-container-breeders. He further notes that members of " the primitive anopheline subgenus *Stethomyia* ", which have a conspicuous white marking in the actual integument, are also among the only American anophel-

ines which fly and feed fairly readily by day. Shannon's work receives confirmation from the observations discussed below. The metallic and strikingly-marked African mosquitoes are mainly diurnal small-container-breeders which do not appear to form swarms. Such are *Aedes longipalpis*, and several members of the subgenus *Stegomyia*. The small-container-breeders of the genus *Eretmapodites* appear to respond visually to the presence of a host (Haddow, 1954, 1956*b*), and in these strikingly coloured and patterned diurnal mosquitoes, where recognition is probably visual, it is noteworthy that the male hind tarsi are sometimes heavily plumed, sometimes in addition bent upward at a sharp angle, and sometimes strikingly tipped with white. In *E. chrysogaster* pairing is known to be an individual matter (Haddow, 1946), and takes place, in cages at least, after the blood-meal (Gillett, 1958). We have also noted a conspicuous display flight in the brilliant, metallic males of *Toxorhynchites brevipalpis* subsp. *conradti*, where a single specimen rises and falls repeatedly over a breeding-place (such as a bamboo container) or carries out a similar flight up and down a vertical feature (such as one of the steel columns of the tower or a tree trunk), in both cases emitting an extremely loud, sustained note. Further, the only brightly-coloured mosquitoes which we have taken swarming were the *Mansonia aurites* group and *M. fraseri*, where the colour is very largely golden. These mosquitoes are, however, active at times when there is insufficient light for the colour to be clearly seen. Again, as in Shannon's observations, the only markedly diurnal *Anopheles* (in the Entebbe area at any rate) is a handsomely coloured species, *A. implexus*, which has an additional striking feature, a row of conspicuous tufts along the sides of the abdomen. Here the females are easily found. They sit in the hollows between tree-buttresses, gently raising and lowering the very conspicuous white-tipped hind tarsi alternately. Thus Shannon's division into (a) metallic or strongly patterned or ornamented species which are mainly diurnal, and small-container-breeders which do not swarm but which may show display behaviour and (b) species mainly drab in colour, mainly nocturnal ground-water-breeders, which do swarm and which do not show display behaviour, appears to hold good in Africa as well as in South America.

As so many well-known workers remain at variance over the function of swarming it appears to us that further study is required before final conclusions can be reached. We would, however, emphasise that the phenomenon occurs in a very large number of species, belonging to widely divergent groups, that it occurs in response to stimuli of various kinds, that the response also is very varied, and that the activity is most persistently maintained. It appears to us, therefore, that whatever its function may be, swarming is unquestionably an activity of major importance to the insects concerned, and we find it difficult to agree with those authors who postulate that it is a vestigial or ritual activity. Perhaps the best comment is that of Nielsen and Haeger (1960) who say " As to the question : Why do mosquitoes swarm? We have to reply : We do not know. It seems to us that the right thing to do is to admit our ignorance and abstain from any guesswork. There was a time when ' everybody knew ' that locusts migrated for want of food. It is significant to us that the recent progress in the analysis of migration in locusts was first achieved after it was realised that migration has no ' purpose ' so far known to us ".

Observations on swarming in African biting Diptera are extremely scarce. Lewis (1943) observed males of *Aedes vittatus* flying in small swarms near the ground by day, in the Nuba Mountains area of the Sudan. Harper (1944) has described evening swarms of *Anopheles funestus* in a mud-and-wattle building. All the specimens taken were males. Muirhead Thomson (1948) has described swarming in *Anopheles gambiae* (or perhaps the var. *melas*). The swarms formed over small palms and shrubs at dusk. One swarm was sampled, no females being found. Lewis (1956*b*) observed a small swarm of *Anopheles cinereus* over a table after sunset. It is interesting that his collection from this swarm included a female *Culex*

theileri. Recently McClelland (1959) has described swarming by males and females of *Ae. aegypti* near ground level, and has noted copulation in one of the three swarms observed. These observations are of particular interest as *Ae. aegypti* is well known as a stenogamic species which in cages mates freely without swarming. It is also one of those species in which males await females near the host—an observation confirmed by other work reported by McClelland in the same paper. The species of *Stegomyia* observed by Lewis to swarm is perhaps the most drably-coloured of the subgenus, but *Ae. aegypti* is a most strikingly-patterned mosquito with much brilliant silver scaling. The writers have been unable to trace other records of mosquitoes swarming in Africa, though Nielsen and Nielsen (1958) have described the swarming of an important African species, *Culex univittatus*, in Iraq. *C. univittatus* in that area swarms over light coloured markers, before sunset.

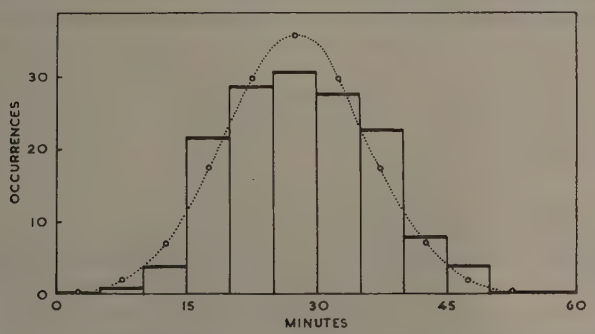

Fig. 1.—The sunset swarming of mosquitoes, Mpanga Forest, showing the number of times that swarming was recorded between 18.00 and 19.00 hours, by five-minute periods, regardless of species. Superimposed is a normal curve fitted to the data. The time scale is in minutes from sunset, which is shown as zero.

The tower on which the present studies were carried out was built close to a tall, emergent tree in the hope that this might act as a swarm marker and that the swarms would be observable from the top platform. As it turned out, however, the tower itself acted as a marker and swarms of insects were formed over it nightly at all seasons, except in the wettest and windiest weather. Thus on 32 evenings' observation, spread over almost a year, swarms formed on 31. Dawn swarms were much less active than those watched in the evening and on cold or wet mornings swarms did not form. Thus insect swarms were observed on only 18 out of 28 mornings and they were always small in size and of short duration.

The foci were various. On the top platform there is a somewhat gallows-like derrick on one side and this was the commonest site for mosquito swarms, though on some occasions swarms formed over the centre of the platform, or over one corner, or over a rail. During the sunrise observations a swarm of small Stratiomyidae was very often seen, always in the same place, a few feet off the side of the platform. Gradually this swarm would move further away, at the same time rising slowly, and in this case it seemed certain that no fixed marker or level was involved after the initial assembly. The mosquito swarms were clearly associated with definite features, and particularly with the vertical limb of the derrick. Biting mosquitoes apparently paid no attention to the presence of swarms and, on evenings when a light-trap was in action, the swarming insects showed no sign of being attracted to it. In these ways the swarming individuals seemed, as it were, detached from the other mosquitoes which were active at the same time. They formed an isolated section of the community orientated, by some response, to the marker and perhaps caught in a " physiological trap " of the type described by Tinbergen (1951).

On most evenings swarming began and ended suddenly. In warm sunny weather the swarms tended to be larger, to contain more species, and to last longer. Nielsen and Nielsen (1958) have recorded, similarly, that when swarms are large they tend to last longer than when they are small. This they attribute to the greater scatter of individual response to the stimuli which lead to swarming. Unfortunately we had no adequate method for estimating the number of insects in a swarm at a given time. In the present work sampling was carried out with a sweep-net, the hour after sunset being divided into five-minute periods. Even when a fixed number of strokes is made this method is not quantitative, as a great deal depends on the position of the swarm. If, for example, it is high overhead, the densest part of the aggregation may be out of reach. The method does, however, permit the presence

TABLE I.—*Dusk and dawn swarming of mosquitoes and tabanids, Mpanga Forest. The table shows the number of occurrence records for each species, by five-minute periods.*

	Total swarm evenings	Dusk periods beginning 18–											
		00	05	10	15	20	25	30	35	40	45	50	55
U. pallidocephala	15	.	.	2	2	9	7	5	4	2	.	.	.
U. alboabdominalis	2	.	.	.	1	1	2	1	1	.	.	.	.
U. chorleyi	1	.	.	.	1	.	.	.	.	.	.	.	.
M. metallica	27	.	1	1	13	20	24	13	7	2	1	.	.
M. versicolor	5	.	.	.	.	.	3	.	2	.	.	.	.
M. pseudoconopas	14	.	.	.	2	6	10	11	7	4	1	.	.
M. maculipennis	1	.	.	.	.	1	.	.	.	.	.	.	.
M. fuscopennata	31	.	1	3	20	28	29	26	22	6	3	.	.
M. aurites	12	.	.	.	1	4	6	4	4	.	.	.	.
M. fraseri	3	.	.	.	.	.	1	3	.	.	.	.	.
Ae. nigerrimus	1	.	.	.	.	1	.	.	.	.	.	.	.
Ae. ingrami	4	.	.	.	3	1	1	.	.	.	.	.	.
C. annulioris	1	.	.	.	.	.	1	1	.	.	.	.	.
H. patellicorne	.	.	.	.	.	.	.	.	.	.	.	.	.
T. thoracinus	.	.	.	.	.	.	.	.	.	.	.	.	.
C. centurionis	.	.	.	.	.	.	.	.	.	.	.	.	.

	Total swarm mornings	Dawn periods beginning 05–											
		00	05	10	15	20	25	30	35	40	45	50	55
U. pallidocephala	6	.	.	.	.	1	3	4	2	.	.	.	.
U. alboabdominalis	1	.	.	.	.	.	.	1	.	.	.	.	.
U. chorleyi	.	.	.	.	.	.	.	.	.	.	.	.	.
M. metallica	.	.	.	.	.	.	.	.	.	.	.	.	.
M. versicolor	.	.	.	.	.	.	.	.	.	.	.	.	.
M. pseudoconopas	.	.	.	.	.	.	.	.	.	.	.	.	.
M. maculipennis	.	.	.	.	.	.	.	.	.	.	.	.	.
M. fuscopennata	5	.	.	.	.	.	3	1	1	.	1	.	.
M. aurites	.	.	.	.	.	.	.	.	.	.	.	.	.
M. fraseri	.	.	.	.	.	.	.	.	.	.	.	.	.
Ae. nigerrimus	.	.	.	.	.	.	.	.	.	.	.	.	.
Ae. ingrami	.	.	.	.	.	.	.	.	.	.	.	.	.
C. annulioris	.	.	.	.	.	.	.	.	.	.	.	.	.
H. patellicorne	2	.	.	.	1	.	1	.	.	.	.	.	.
T. thoracinus	4	.	.	.	.	2	1	1	.	.	.	.	.
C. centurionis	2	.	.	.	.	1	1	.	.	.	.	.	.

or absence of different species to be established on a closely subdivided time-scale, and the work here discussed is thus concerned with the number of occurrences rather than with the number of insects present. On occasion the mosquitoes were, however, counted, as sweep-net sampling enables an estimate to be made of the male : female ratio.

One of the objects of work on the tower was to find whether there was much mosquito activity above the forest in the period after sunset, when thermal currents might carry small insects to great heights (Wellington, 1945 ; Haddow *et al.*, 1951). The present series of observations shows that there is a period of intense activity on almost every evening at this time. Further, on two occasions, very large swarms rose out of sight as darkness deepened, and were last seen 70–80 feet above the top of the tower and thus about 200 feet above ground level.

The earliest swarming activity recorded was in the second five-minute period after sunset, 1805–1809 minutes, and the latest in the tenth such period, 1845–1849. When the results for all species combined are considered, the histogram shown in figure 1 is obtained. This shows that swarming activity is very symmetrically disposed about a mode in the period 1825–29, when 21 per cent. of all recorded activity took place. If the periods before and after this be included, it is found that 58 per cent. of all swarm occurrences fell within these limits, *i.e.* between 1820 and 1834.

In figure 1 a normal curve has been fitted to the observed data. Though at first sight the fit appears a good one, it is in reality very poor indeed, P being $<\cdot01$. If we accept the standards of Croxton and Cowden (1948), then P values of $<\cdot05$ are to be regarded as indicating that the distribution is not a normal one. In the present instance the main divergence is the flattening of the top of the curve around the modal period. This, we believe, may be due to the fact that in this investigation occurrences, not the number of insects, were the unit of measure. Though we are unable to produce definite evidence, we have a strong conviction that on most nights the numbers of insects in the swarms, small at first, increased gradually to a modal point and thereafter diminished. Perhaps, had it been possible to count the insects in the swarm period by period, a normal curve might have resulted.

The detailed results, by species, for evening and morning swarming are given in Table I. The evening swarms will be discussed first, with reference to the more abundant species. As mentioned above the swarms almost always consisted of several mosquito species, and members of other groups were frequently present, small Tipulidae being particularly common in the evening catches. The swarms, so far as mosquitoes were concerned, were made up as follows :

Number of species represented in the swarm	Number of evenings
1	2
2	8
3	8
4	2
5	2
6	6
7	3

As will be shown below, however, the time of onset and ending was not the same in all species.

Uranotaenia pallidocephala was observed swarming on 15 evenings. The duration of the swarms was 5–25 minutes, with a mean in the 10–15 minute group. The usual time of onset was in the period 1820–1824, swarms beginning at this time on 7 out of the 15 evenings on which they were recorded. As shown in figure 2, the modal period was clearly marked, occurring in the period 1820–24. The ending of the swarms was irregular.

Mansonia metallica swarmed very regularly and was observed on 27 evenings. The duration of the swarms was 5–35 minutes, the usual duration being three five-minute periods. Once again the peak period was clearly marked, occurring in the period 1825–29, five minutes after that for *U. pallidocephala*. As is shown in figure 2, swarming is more frequent before this period than after it. On 12 evenings swarming ended in the period 1825–29, on 6 in the period 1830–34 and on 5 in the period 1835–39. Thus on 23 of the 27 evenings swarming ended in the period 1825–39.

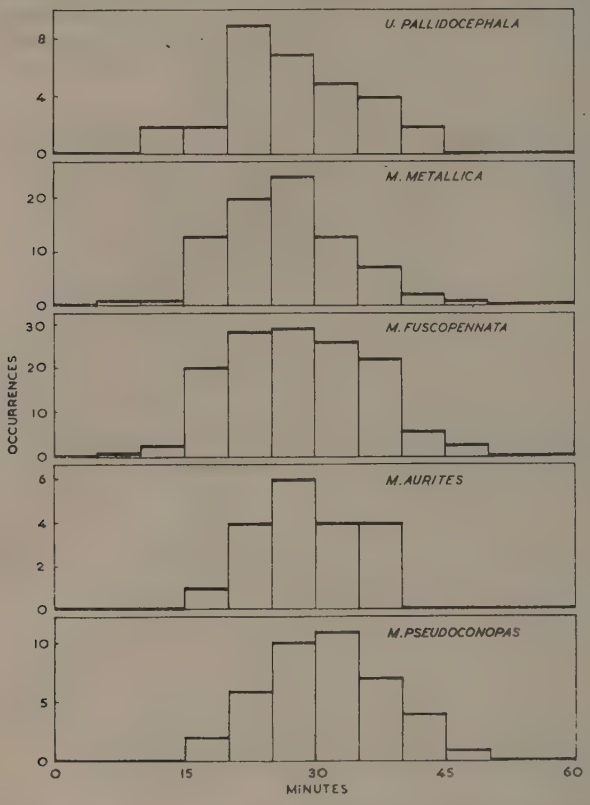

FIG. 2.—The sunset swarming of 5 common mosquito species, by five-minute periods. The histograms show the number of occurrences per period. The time scale is in minutes from sunset, which is shown as zero.

M. fuscopennata was the dominant swarming species, and was taken on 31 evenings. The duration of the swarms varied from 5–35 minutes, the commonest duration being four to five five-minute periods. The usual time of onset was 1815–19, swarms beginning at this time being recorded on 17 occasions, and the commonest time of ending was 1835–39, swarms ending at this time being recorded on 15 occasions. Where the peak period with reference to the time of sunset is concerned, 1825–29 was, as in the case of *M. metallica*, the preferred time, but while in *M. metallica* swarming was more frequent before than after this period, in *M. fuscopennata* it was very symmetrically disposed about it and thus the trend with reference to sunset was, if anything, later.

M. aurites swarms were recorded on 12 evenings. The duration of swarming was 5–25 minutes, with a mean in the 5–10 minute group. On 8 of the 12 evenings

the swarms were of this very short duration. The swarming peak occurred in the same period as that for *M. metallica* and *M. fuscopennata* namely, 1825–29, but here there were more records after than before the mode, and so the main tendency was probably to swarm a little later than *M. fuscopennata* and distinctly later than *M. metallica*. The number of records is not adequate for a discussion of the usual times of onset and ending of the swarms, but it is interesting to note that swarming was never recorded till the period 1815–19.

M. pseudoconopas was observed swarming on 14 evenings. The duration of the swarms varied from 5–20 minutes, the commonest duration being four five-minute periods. The peak occurrence of swarms was later than in the other species discussed, occurring in the period 1830–34 and, as in the case of *M. aurites*, swarming began late, the earliest records being for the period 1815–19. The beginning and ending of the swarms was rather irregular, and a longer series of observations would be necessary to delimit them.

TABLE II.—*The habitual periods for the onset and cessation of swarming in the commoner species, considered in relation to the onset and cessation in* M. fuscopennata, *which is here recorded as zero.*

Onset

Species	−15	−10	−5	0	5+	+10	+15	+20	+25	+30	+35
M. metallica	.	1	.	15	10	1	.	.	.	.	.
U. pallidocephala	.	.	1	2	6	3	1	1	1	.	.
M. pseudoconopas	.	.	.	2	6	2	3	1	.	.	.
M. aurites	.	.	.	1	3	4	1	3	.	.	.

Cessation

Species	−35	−30	−25	−20	−15	−10	−5	0	+5	+10	+15
M. metallica	.	1	.	1	2	8	3	14	2	1	.
U. pallidocephala	.	.	.	.	4	3	2	6	.	.	.
M. pseudoconopas	.	.	.	.	.	3	3	6	2	.	.
M. aurites	.	.	.	.	.	.	2	6	3	1	.

So far, the analysis has been carried out with reference to the time of sunset, which is obviously an extremely important factor. Nielsen and Nielsen (1958) have here made a major contribution in pointing out that swarming is related to the actual time of sunset rather than to its apparent time; thus the presence of a cloudbank, cutting off direct sunshine before the true horizon is reached does not affect the time of swarming. It is therefore the zenith light which is of importance. This matter will be discussed further below, and for the moment it is enough to record that the writers are in agreement with the Nielsens, and feel that zenith light must be regarded as the crucial factor, though wind and unfavourable temperatures may of course have inhibitory effects.

While the foregoing analysis shows the general trends of swarming behaviour in the more abundant species, it does not show the sequence of events on particular evenings. Thus the fact that species A reaches its swarming peak later than species B does not necessarily mean that A habitually begins swarming later than B. It may, for example, begin swarming at the same time as B but in a skew distribution reach its modal peak either before or after B. Similarly, even if the distribution is symmetrical it may begin to swarm at the same time as B and reach the peak later than B if the habitual duration of its swarming is the longer of the two.

There is thus some interest in studying the time relationships of swarming in the commoner species with reference to one another rather than to sunset. This can be done only by fixing reference points which can be applied to each evening's observations separately. In this paper the reference points will be the beginning

and ending of swarming in the commonest species, *M. fuscopennata*, which swarmed on every evening on which this activity was seen. It is presumed that these points have some real biological significance, presumably response to environmental factors. Once established in a given individual insect, such responses will tend to be repetitive, as it has been found that persistent endogenous circadian rhythms (see Part I, p. 253) do occur in mosquitoes (Haddow, Gillett and Corbet, 1961).

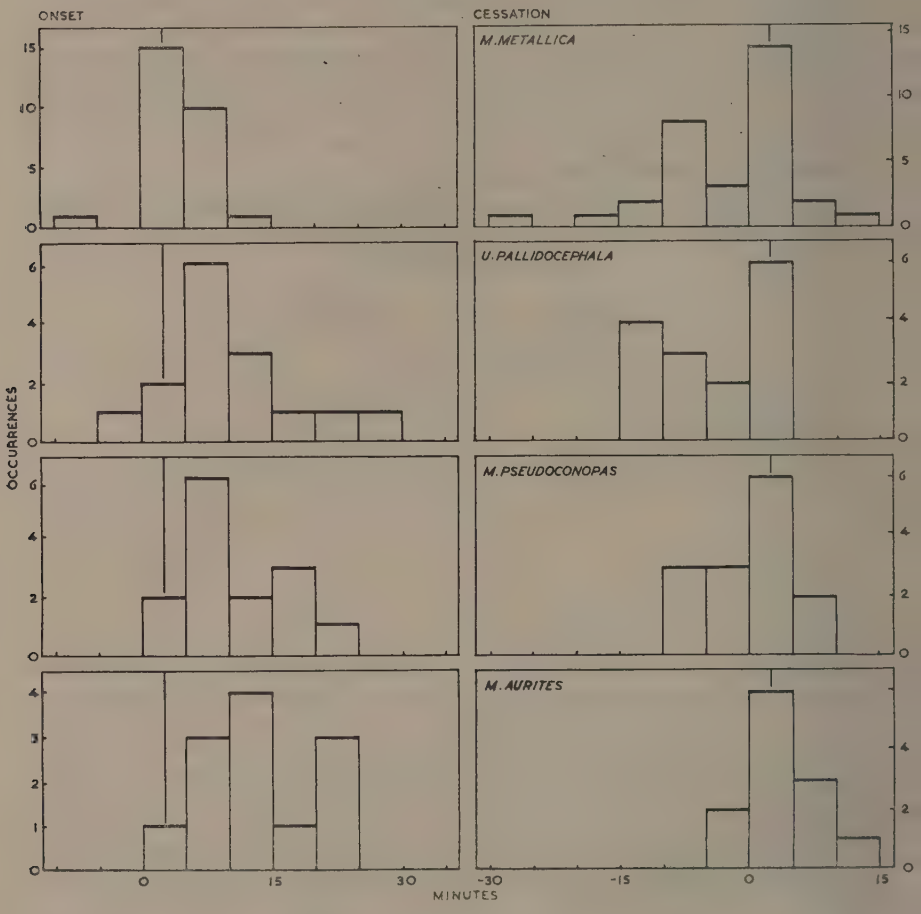

FIG. 3.—The onset and cessation of swarming in 4 common species, by five-minute periods. The reference point, shown by a vertical line, is the onset or cessation, as the case may be, in the most abundant species *Mansonia fuscopennata*, with which the others are here compared. The histograms show the number of occurrences of onset or cessation per five-minute period. The time scale is in minutes from the onset or cessation in *M. fuscopennata*.

Of course, *M. fuscopennata* having been taken as the standard, it itself is to some extent eliminated from discussion. In future work it is planned that some other biological phenomenon will be used as a point of reference. Certain frog and insect choruses, for example, occur with remarkable consistency in the tropics at about the time that swarming begins, and one of these might be suitable.

The results (Table II ; fig. 3) show that, where the onset of activity is concerned,

M. metallica only once began to swarm earlier than *M. fuscopennata*. The modal time of onset (relative to that of *M. fuscopennata*) was distinct, and was in the same period as that of *M. fuscopennata*. In *U. pallidocephala* also there was one record of onset before that of *M. fuscopennata*, but the well-marked mode for time of onset did not occur till five minutes after that for *M. fuscopennata* and *M. metallica*. *M. pseudoconopas* was not recorded on any occasion as swarming before *M. fuscopennata*, and the modal time of onset was in the same period as that for *U. pallidocephala*. The number of records for *M. aurites* was very small, but here the mode was probably later still. There is thus a distinct serial tendency in the onset of swarming in these species, *M. fuscopennata* and *M. metallica* being first, *U. pallidocephala* and *M. pseudoconopas* second, and *M. aurites* probably last.

For cessation the picture is entirely different, as here all species tend to end swarming in the same period as *M. fuscopennata*. This suggests that a threshold light value may be involved, possibly that below which the marker no longer presents an adequate visual stimulus to retain these insects in swarm formation.

With reference to onset, some comments on the changes in light in the sunset period are indicated. Near the equator, where the work was carried out, the daily march of light intensity in the open shows a rather flat-topped curve. Shortly before sunset a very rapid fall in intensity begins. At first the rate of change increases, but after sunset it becomes remarkably constant, at least during the first forty minutes or so. The trend is well shown by a series of readings made at Entebbe on a single clear evening, which may be summarised as follows:

10-minute period beginning	Mean percentage decrease per minute
−40	0·9
−30	2·9
−20	3·7
−10	7·8
0 (Sunset)	8·0
+10	9·4
+20	9·4
+30	9·1
+40	9·1

Further studies on light in the sunset period are now in progress, very sensitive photometers being employed. This work is far from complete, but some major points may be discussed briefly. The Entebbe area, lying in the zone of atmospheric turbulence which extends along the north shore of Lake Victoria, is generally rather cloudy, even in dry weather. In the west the horizon is habitually obscured by low cloudbelts in the evening, and in general light readings at sunset are low, rarely exceeding 50 foot-candles (538 lux), and sometimes being less than 10 (108 lux). At the equator, where these studies are being carried out, Astronomical Twilight, theoretically complete darkness, occurs 72 ± 3 minutes after sunset, when the sun is 18° below the horizon (the fluctuations are seasonal). The photometers at present available allow readings to be made during the first forty to fifty minutes of this period. The preliminary series show that, if sunset light be considered as 100 per cent., the main features of the swarming period are as follows:

The earliest swarm we have recorded began in the period +5 to 9 minutes. By the middle of this period the light has fallen to a quarter of its sunset value. It is usually under 10 f.c. (108 lux), and may be under 5 f.c. (54 lux). Swarming at such a time is, however, unusual and the modal time of onset was in the period +15 to 19, when activity began on 18 of the 31 evenings on which swarms were formed. By +15 minutes the light has fallen to less than 5 per cent. of its sunset value and is

frequently under 1 f.c. By the end of this five-minute period it is approximately 2 per cent. of the sunset value. Swarming reaches its peak in the period +25 to 29, and during this period the light intensity falls to about 0·1 per cent. of the sunset value. The modal period for cessation was in the period +35 to 39. The indicators on the photometers at present available are at this time reaching the bottom of their readable scale and our observations are not as accurate as could be wished, but the work so far carried out suggests that at this time the light intensity has fallen to something like 0·001 per cent. of the sunset value. Work on light readings continues, in the hope that it may be possible to produce a curve which, within a few degrees of the equator, will enable the observer to deduce from a single reading at sunset approximate values for the critical periods which follow, and so to concentrate his attention on the observation of the insects rather than on the photometer.

These results suggest that there may be some upper threshold value above which swarming in the species we have studied does not occur. Obviously, however, onset does not occur at a fixed light intensity. This observation is in agreement with the findings of Nielsen and Greve (1950) on *Ae. cantans* and with those of Senior White *et al.* (1953) on *A. aquasalis*. The latter authors have given a most satisfactory demonstration that the onset of swarming, while it does not occur above a certain light threshold, is very closely related to the time of sunset, and not to a particular level of illumination. Their results show that on 25 per cent. of evenings *A. aquasalis* began to swarm in the extremely narrow period +19 to 24 minutes, and on 67 per cent. it ended in the period +33 to 38. Equally close grouping for onset occurs in the biting behaviour of certain species such as *M. fuscopennata* and *Aedes africanus* (Haddow, 1956*b*) which show peak activity in the crepuscular period. In such cases the scatter of the observations with reference to the time of sunset is so small that it cannot be explained on the assumption that activity begins at a particular light value. It can, however, be explained as occurring at a certain time after sunset, always provided that light has fallen below a certain upper threshold, which may differ from species to species. In this connection it is important to remember that at the equator the rate of loss of light after sunset is so great and the whole crepuscular period so short that frequently, as noted above, the intensity will have dropped to about 1 f.c. (9 lux) within 15 minutes of sunset. Further and more detailed work on this whole aspect of the subject is planned, and at the moment the writers feel that it would be premature to commit themselves to a definite view where relationship of light intensity to the onset of swarming is concerned. Cessation is, as noted above, probably more easily explained, and may well depend on a threshold light value below which visual stimuli become inadequate. Present work suggests that if there is such a threshold it may lie in the neighbourhood of 0·005 f.c.

Females were taken on 19 occasions in evening swarms. The species were *U. pallidocephala*, *Ficalbia* sp. indet.*, *M. metallica*, *M. versicolor*, *M. pseudoconopas*, *M. fuscopennata*, *M. aurites*, *M. fraseri*, *Ae. africanus**, *C. annulioris* and *Culex* (*Culex*) sp. indet.* Thus 11 species were taken. Three (marked by asterisks) were not represented as males in the swarms throughout the entire investigation, and it is of course possible that these may have occurred by chance. With reference to regularity of occurrence, it may be stated that though females of one species or another were taken on several evenings, the only species which yielded numbers large enough for individual consideration was *M. fuscopennata*, of which females were taken on 13 evenings (as opposed to 31 for the males).

As mentioned above, the sweep-net samples were counted on a number of evenings to establish the ratio of males to females. The results were surprising, revealing that the ratio varied widely from one species to another. The detailed figures were as follows :

Species	Number of males taken	Number of females taken	Ratio	Females as percentage of total catch
Ae. ingrami . .	20	0	.	.
M. metallica . .	704	4	176 : 1	0·6
U. pallidocephala .	62	1	62 : 1	1·6
M. pseudoconopas .	199	4	50 : 1	2·0
M. fuscopennata .	1091	31	35 : 1	2·8
M. versicolor . .	8	1	8 : 1	11·1
M. aurites . .	14	13	1 : 1	48·1
M. fraseri . .	6	19	1 : 3	76·0
Total . .	2104	73	29 : 1	3·5

Females thus formed 3·5 per cent. of the counted sample, a figure in accord with those given by several other workers. The striking feature is the extraordinarily high proportion of females among the golden *Mansonia* (*Coquillettidia*) spp. of the *aurites-fraseri* group. These mosquitoes are markedly arboreal and crepuscular and it has been shown by Williams *et al.* (1958) that they feed mainly on birds. Of the 52 mosquitoes in this group, 32 (or about 62 per cent.) were females. This observation is unprecedented, we believe, in records of bisexual mosquito swarms.

On no occasion have the writers observed mating in the swarms above the forest. As this is a conspicuous activity with which both of us are familiar in other insect swarms we believe that in the mosquito swarms we observed it cannot have occurred except rarely and could not account for more than a minute fraction of the mating activity in the area concerned, where females of some of the species concerned are known to be present in vast numbers. In this connection it is interesting to consider once more the observations of other workers. Review of the literature reveals that many records of active mating in swarms refer to anophelines. While mating has often been recorded in swarms of culicines, in which a really active approach by the female is described (for example, Hearle (1929) on *Ae. flavescens* and Wesenburg-Lund (1920) on *Ae. communis*), there is unfortunately no clear statement as to the number of females entering the swarms. The *Culex pipiens* group is perhaps unique in this respect, as several workers have described very active mating in swarms. The males, however, will also mate readily in cages without swarming at all.

It seems obvious that each species or group of species must be treated individually where mating in swarms is concerned, and that no general rule can be laid down. One aspect that we feel has received quite inadequate attention is the effect of swarming on the males themselves. In some insects at least the action of the wings raises the body temperature very substantially (for convenient summaries *see* Wigglesworth, 1950 and Roeder, 1953) and this itself may have an effect on reproductive potency, whether mating occurs at the time of swarming or subsequently. It is most necessary to remember that sexual maturity and sexual potency are entirely different things, and that in many groups some form of collective behaviour is necessary before copulation is effectively achieved. This is the case in many tropical weavers, and Fraser Darling (1938) has shown that in some marine birds effective reproduction depends on the size of the colony and may fail altogether if this falls below a certain level. While, as noted above, a single insect may exhibit swarming behaviour, the object must in the end be to gather a group of insects collectively performing the same kind of flight in response to a particular stimulus, and it is felt that the physical effects of this flight on the males clearly call for further study.

Swarming at dawn may be dealt with briefly as it is essentially similar to sunset swarming. The main difference between the dawn and sunset period is in temperature. It is well known that the flight of many insects is inhibited by low temperatures, and this may be the reason why swarms at sunrise are of much less regular occurrence than those at sunset (Table I). Only once was a female taken.

Not only were the dawn swarms less regular in occurrence; they were smaller

and of shorter duration. This is in agreement with the findings of Nielsen and Nielsen (1958) in Iraq, which have already been mentioned. Thus the greatest duration of dawn swarms in *U. pallidocephala* was 15 minutes, and in *M. fuscopennata*, 10 minutes. The main time of swarming bore much the same relation to sunrise (approximately 0555 hours) as did the evening swarming to sunset, reaching its peak about half an hour before this event. Thus, when the results for all species are combined to give a general table of the occurrence of swarming activity, the following figures are obtained.

Minutes before sunrise	Number of occurrences
59–55	.
54–50	.
49–45	.
44–40	.
39–35	1
34–30	5
29–25	5
24–20	2
19–15	.
14–10	1
9–5	.
4–0	.

The most striking feature of the period before sunrise was the swarming of tabanid males. While the swarms were never composed of more than a few individuals, the characteristic " swarming flight " was always most obvious, sometimes a vertical and sometimes a horizontal zig-zag pattern being followed. The swarms were usually too high above the platform for capture to be attempted. In addition the flies were extremely wary, and one or at most two sweeps of the net were enough to disperse the swarm for the time being. The powerful hovering flight and deep hum of the tabanids was a most interesting feature of the sunrise period and, though few were actually captured, the appearance, duration and cessation of the swarms could be recorded. They were frequently mixed, as was shown by actual captures and also by direct observation, as sometimes tabanids of very varied sizes took part. The largest of these, almost certainly a member of the genus *Ancala* or *Tabanus*, was never captured. It always took up a position 15–20 feet above the platform, and so was out of reach. It is interesting that the actual captures all occurred in the early part of the swarming period. Possibly at this time the insects were not fully warmed up by flight and were more easily taken.

Tabanid swarms were observed on 15 mornings and, though captures were achieved on 7 of these only, a general graph of swarming activity, based on captures and sight records, can be constructed (fig. 4). The curve is skewed, but shows a well-defined mode in the period 0530–0534, *i.e.*, about half an hour before sunrise. Though Bailey's (1948) summary of work on the swarming and mating of Tabanidae shows that many species mate in the morning, no general rule can be given, as Haseman (1943) has discussed this activity in two species, one of which (*Tabanus sulcifrons*) swarms, like the species encountered at Mpanga, before daybreak, while the other (*T. giganteus*) swarms at dusk. The records concerning *T. sulcifrons* are of particular interest in the present connection as the swarms occurred high above the ground, usually at treetop level. The flights began at about 5.30 a.m., just at daybreak, when the light intensity was under 1 f.c. (9 lux), and went on for 20–25 minutes, ending at 3–5 f.c. (32–54 lux). Females were on the wing at this time but did not fly at the same level, being active over grass and low shrubs. They did not join the swarms and it is known from another source (Hine, 1960) that *T. sulcifrons* mates later in the morning, between 8 and 9 a.m. Thus, as in the case of the mosquitoes, there is some doubt as to whether swarming and mating are directly associa-

ted. Blickle (1959), however, has noted that in the sunrise swarms of *Tabanus bishoppi*, which occur at canopy level, mating frequently occurs. On one occasion at least 20 males from a swarm of 25 were observed to mate.

Haseman's observations have been discussed critically by Craig (1944) who points out that bird song, not closely associated with mating, occurs both at dawn and at sunset. He suggests that the problem might be investigated by finding if *T. sulcifrons* ever swarms in the evening, or *T. giganteus* in the morning. In this connection our present findings are of interest as in the species observed by us swarming was entirely a dawn activity. At sunset we occasionally saw a tabanid sitting on the platform rail or saw or heard one pass, but we saw no swarming activity. Thus swarming in tabanids appears to occur once only in each 24-hour period in the Mpanga area.

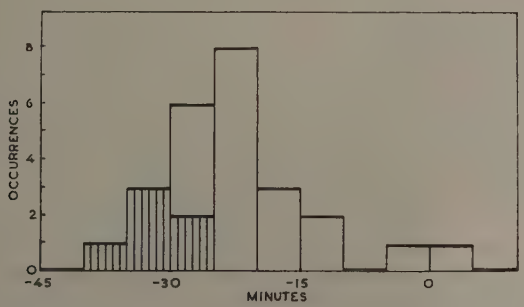

Fig. 4.—The swarming of tabanids at dawn, from sight and capture records, regardless of species, showing the number of times that swarming activity was recorded, by five-minute periods. The shaded part of the histogram shows the number and disposition of records based on specimens actually captured. The time scale is in minutes from sunrise, which is shown as zero.

The eyes of male tabanids are often very remarkable, with an upper area of large facets, and a lower area of small facets, and the colours are frequently very striking. The facets of the lower area approximate in size to those of the female and are usually identical in colour to the eye of the female of the same species. It has been pointed out (Haddow *et al.*, 1950) that many tabanids are nocturnal or crepuscular and that their brilliant and remarkable eye colours and other ocular modifications may have a relation to nocturnal activity or to mating. The late Dr. W. E. Snow (*personal communication*) informed us that male tabanids may fly upside down before mating, the females being above them. This agrees with a statement made by Mosier (concerning males of *Tabanus americanus*) which is quoted by Bailey (1948). If this is the case, then the structure of the male eye becomes more easy to comprehend. Perhaps the upper area with its large facets and coarse resultant image may be adequate for flower feeding, but when the precision involved in the capture of a female is required the other area with its smaller facets (giving an image of the same type which allows her to hunt active prey) becomes necessary. In an attempt to settle this point we have watched the male swarms at dawn through field glasses, but in the extremely poor light prevailing at the time of swarming we have not been able to determine in which position the males were flying. It is interesting to recall Downes' (1958) discussion on the eye-structure of male simuliids, which has been summarised above (p. 287) and it is suggested that further investigation would be desirable in the case of insects where the males have eye-facets of more than one kind, to determine the flight posture in swarms.

A few notes on the species actually taken in swarms may be given. Other work at Mpanga, which will be discussed separately, has shown that the females of *Haematopota patellicorne* are active by night. None has so far been taken above ground level, but a male was taken above the forest in a light-trap. *Tabanus thoracinus* males have been known to have nocturnal propensities for some time past (Haddow, 1952) and recently light trap-catches (Haddow and Corbet, 1960) have shown that they are on the wing throughout the night, showing a major wave of activity in the periods 03–05 hours, *i.e.* the two hours before the swarming period. *Chrysops centurionis* is well known as an arboreal tabanid which bites in the canopy in the hour after sunset and which probably feeds mainly on monkeys (Haddow and Dick, 1948 ; Haddow *et al.*, 1950 ; Haddow, 1952 ; Duke, 1958 ; Duke and Wijers, 1958). In the light-trap catches referred to above females were taken only in the early night, but males were taken at irregular intervals from dusk till dawn. These findings taken together with the swarming observations confirm the growing opinion that tabanids generally show much more nocturnal activity than was previously suspected.

As with mosquito swarms, the writers feel that the time is not yet ripe for any definite conclusion about the function of swarming in Tabanidae. It is a great pity that much of the recent literature is written in support of one viewpoint or another, sometimes almost in a partisan spirit, when clearly so much more direct observation of the insects and their environment is required before the function of swarming can be fully understood. We cannot do better than conclude by quoting Nielsen (1958).

" Ethology, however, deals not only with the problem of why animals behave as they do, but first of all with *what* animals are doing, then *when* and *how* they are doing it, and finally *why* they are doing it.

" In ' modern ' ethology nobody pays the slightest attention to anything but the ' why ' . . . . But a student of insects cannot help thinking of our miserable ignorance. There is probably not more than one insect species in ten thousand for which our present knowledge permits us to give a fairly complete answer to the question of what it is doing ; and it is doubtful if there are any species of insect for which we can explain satisfactorily all questions of what and when and how.

" To gather such information requires an army of investigators but only a few cranks and amateurs are doing it ".

Summary

1. Mosquito swarms form almost nightly over a 120-foot tower in the Mpanga Forest, Uganda. Several species usually swarm together, and members of other insect groups may also be present. Different species may begin swarming at different times, but all tend to end swarming at about the same time. Evening swarming is confined to the single hour after sunset with a peak in the period 20–35 minutes after sunset. The light changes in the post-sunset period are discussed in relation to swarming behaviour.

2. Dawn mosquito swarms occur with less regularity. They are small and of short duration, and only a few species are involved. At dawn, however, male tabanids of various species swarm regularly over the forest.

3. Mating was not observed, though females were regularly present in the mosquito swarms. Taking all species together, the percentage of females was small, but the sex ratio varied from one species to another and in some cases the females outnumbered the males.

4. Some of the more important literature is reviewed and the function of swarming is discussed, but the conclusion is reached that there is not yet sufficient evidence for an explanation of the phenomenon.

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

VI. NOCTURNAL FLIGHT ACTIVITY OF CULICIDAE AND TABANIDAE AS INDICATED BY LIGHT-TRAPS

By Philip S. Corbet

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Introduction

That mosquitoes are attracted to light at night has long been known, and has led to the development of traps of various kinds. Most light-traps in use to-day embody the principal features of the New Jersey trap (Headlee, 1928, 1932; Mulhern, 1934, 1942), in which insects are first attracted to a point light-source, and then drawn into a killing receptacle by a fan.

Light-traps have been much used, particularly in North America, for studies of biting Diptera, and the literature on this subject is now extensive. Whereas it would be out of place to review this work here, certain findings which are relevant to the present study may be briefly mentioned.

It is characteristic of light-trap catches that they include both sexes of Culicidae (Headlee, 1928), Tabanidae (MacCreary, 1940) and Simuliidae (Vargas, 1945), and that relatively more males are caught if the light is of high intensity (*e.g.* Pratt, 1944) or wavelength (Vargas, 1945). It also appears that a trap in which the bulb is surmounted by an opaque roof (Williams, 1924) is more effective, though not invariably so (Frost, 1958), for catching small, weakly-flying insects (Williams, French and Hosni, 1955), perhaps because, whereas the heavier insects enter a trap largely by their own inertia (Robinson and Robinson, 1950), the lighter ones tend to form columns above an exposed bulb (Corbet and Tjønneland, 1955) or else to settle nearby. It is probably for this reason that a fan, although not essential, greatly increases the numbers of mosquitoes caught (Headlee, 1932; Breev, 1958).

During the present series of investigations, made on a high tower in the Mpanga Forest (Part I), light-traps were used in order to study patterns of flight activity in mosquitoes of both sexes, and to compare these with patterns of female biting activity (*see* Part VII). Earlier studies with light-traps made by other workers elsewhere have demonstrated that recurrent patterns of flight activity exist in mosquitoes (*e.g.* Bradley and McNeel, 1935; Thurman and Thurman, 1955; Breev, 1958; Corbet and Haddow, 1961) and in tabanids (Haddow and Corbet, 1960), and that, in mosquitoes, activity may vary significantly according to height above ground, both inside forest or woodland (Hingston, 1932; Blanton, Galindo and Peyton, 1955; Love and Smith, 1957) and in exposed situations (MacCreary, 1941). Apart from the work at Mpanga, to be described here, I know of no study with light-traps in which flight activity and vertical distribution have been investigated hourly in a forest environment.

Methods

Five light-traps were placed on the tower at Mpanga, at ground level, 30 feet, 60 feet, 90 feet and 120 feet, respectively. The 90-foot trap was just above the forest canopy.

Fifteen collections were made at approximately weekly intervals between 25th September, 1958 and 13th January, 1959. On every occasion the five traps were

run simultaneously and the catch in each was examined hourly. No catches with human bait were made on the tower at times when light-traps were operating. The first two collections each continued for 24 hours, but as the traps caught only very

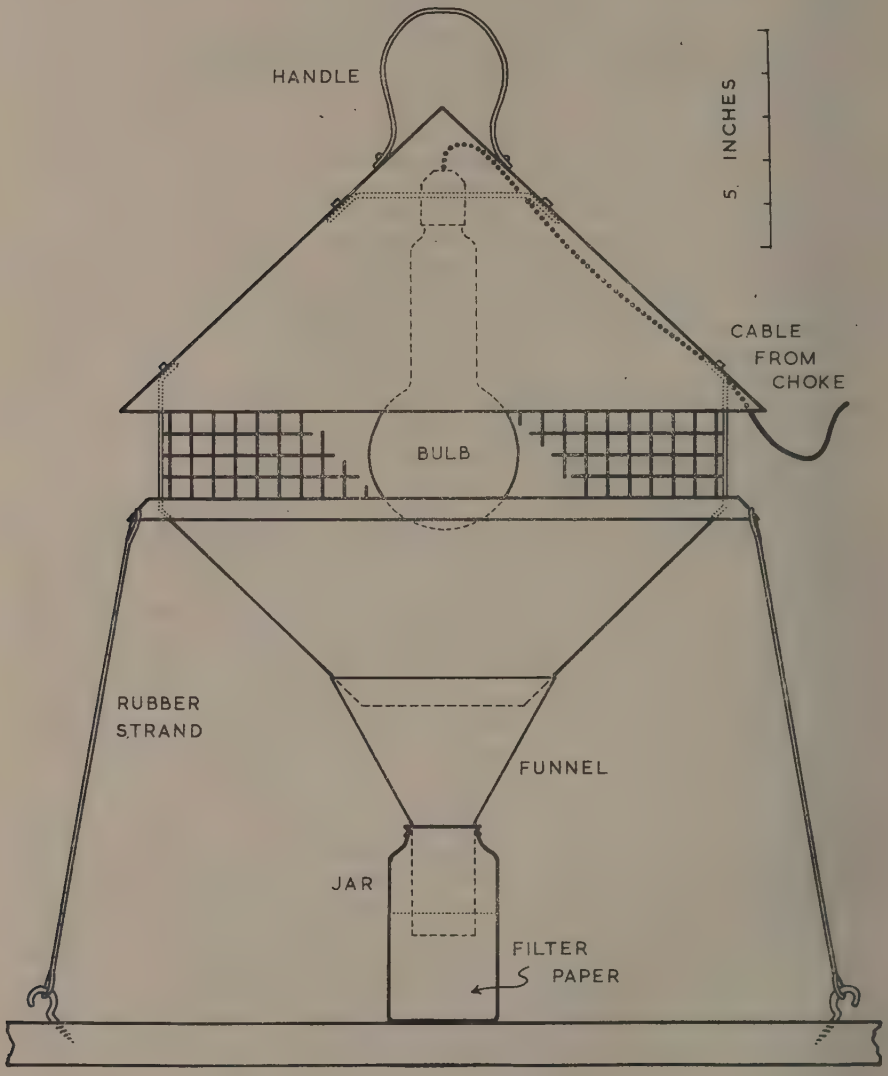

FIG. 1.—Diagram of light-trap used at Mpanga.

few mosquitoes and tabanids during daylight hours, subsequent catches extended only for 14 hours—from an hour before sunset to an hour after sunrise—this period being designated as 17–07 hours " catch time ", according to the procedure suggested by Lumsden (1952).

The design of the trap (fig. 1) incorporated features of both New Jersey and Robinson traps (Mulhern, 1934 ; Robinson and Robinson, 1950). Light was emitted

TABLE I.—*Light-trap catches of male and female mosquitoes at five levels*

Species	Males						Females					
	Levels (feet)						Levels (feet)					
	120	90	60	30	G.L.	Totals	120	90	60	30	G.L.	Totals
Anopheles coustani	1	.	.	.	.	1	.	.	.	.	.	.
A. coustani ziemanni	.	1	.	.	.	1	.	.	.	.	.	.
A. obscurus	.	.	.	1	.	1	.	.	.	.	.	.
Uranotaenia pallidocephala	1	2	.	2	1	6	7	2	1	3	4	17
U. aff. *pallidocephala*	1	.	1	3	.	5	.	.	.	.	.	.
U. alboabdominalis	.	.	.	4	3	7	2	.	2	.	.	4
U. balfouri	.	.	.	.	.	.	1	.	1	.	.	2
U. chorleyi	.	.	2	.	.	2	.	.	2	.	.	2
U. hopkinsi	.	.	.	.	.	.	.	1	.	.	.	1
U. candidipes	.	.	.	.	.	.	1	.	.	.	.	1
U. nigromaculata	.	5	10	13	3	31	.	.	.	1	1	2
Ficalbia hispida	+	+	.	.	.	+	+	+	.	.	.	+
F. uniformis	+	+	+	+	+	+	+	+	+	+	.	+
Ficalbia (all spp.)	+	+	+	+	+	19	+	+	+	+	.	25
Mansonia metallica	34	111	101	70	27	343	10	16	15	22	3	66
M. versicolor	4	4	4	2	1	15	.	.	.	.	.	.
M. pseudoconopas	3	18	45	35	31	132	1	3	3	3	1	11
M. maculipennis	5	17	16	18	11	67	1	2	1	2	1	7
M. fuscopennata	108	98	54	33	42	335	18	7	15	17	21	78
M. aurites group	.	.	1	1	.	2	1	1	.	.	.	2
M. fraseri	45	79	65	30	19	238	5	7	8	2	.	22
M. uniformis	1	.	.	.	.	1	.	.	.	.	.	.
Aedes ingrami	.	1	2	3	8	14	.	.	.	.	.	.
Ae. apicoargenteus	.	.	.	.	.	.	.	.	.	2	.	2
Ae. dendrophilus	.	.	.	.	1	1	.	.	.	.	.	.
Ae. africanus	.	.	.	.	1	1	.	.	.	.	.	.
Ae. capensis	.	.	.	1	1	2	.	.	.	.	.	.
Ae. haworthi	.	.	1	.	.	1	.	.	.	.	.	.
Ae. argenteopunctatus	.	.	1	.	1	2	.	.	.	.	.	.
Ae. aff. *mixtus*	1	.	.	.	.	1	.	.	.	.	.	.
Ae. mutilus	.	.	1	1	.	2	.	.	.	.	.	.
Ae. leptolabis	1	1	.	1	.	3	.	1	.	2	.	3
Ae. tarsalis	.	.	.	.	1	1	.	.	.	.	.	.
Ae. circumluteolus	1	6	3	2	3	15	.	.	.	.	.	.
Ae. taeniarostris	.	.	1	.	.	1	.	.	.	.	.	.
Ae. palpalis	1	3	2	2	.	8	.	.	.	.	.	.
Culex tigripes	.	1	3	.	1	5	.	.	.	.	.	.
C. kingianus	.	.	.	+	.	+	.	.	.	.	.	.
C. insignis	3	53	102	78	91	327	4	10	10	7	4	35
C. horridus	.	.	+	.	.	+	.	.	.	.	.	.
C. nebulosus	.	.	.	.	+	+	.	.	.	.	.	.
C. cinereus var. *uniformis*	.	.	.	+	.	+	.	.	.	.	.	.
C. cinerellus	.	+	.	.	.	+	.	.	.	.	.	.
C. semibrunneus	.	.	+	.	+	+	.	.	.	.	.	.
C. annulioris	1	2	2	2	1	8	.	.	.	.	.	.
C. pruina	.	.	.	.	1	1	.	.	.	.	.	.
C. moucheti	1	.	.	.	.	1	.	.	.	.	.	.
Culex spp. indet.	1	16	14	8	9	48	1	5	6	11	.	23
Totals						1648						303

horizontally as a narrow beam, to minimize interference between traps at adjacent levels. The conical roof, necessary to achieve this, may also have increased the efficiency of the trap for collecting mosquitoes. For the fourth and subsequent catches, a wire screen of $\frac{3}{8}$-inch mesh was placed around the entrance of each trap to exclude large insects.

The light consisted of a 125-watt mercury-vapour bulb, as used in a standard Robinson trap. A generator, situated on the forest floor about 30 yards from the tower, supplied electric power. A cable carried the current to the base of the tower, where it entered a portable box containing a choke for each of the five lamps. Five cables of equal length (*ca.* 130 feet) ran from each choke to its corresponding trap. Switches on the choke box enabled all traps to be controlled independently at ground level. Unfortunately, there was not enough power to operate a suction fan on each trap. Failure of the generator restricted the series to 15 catches.

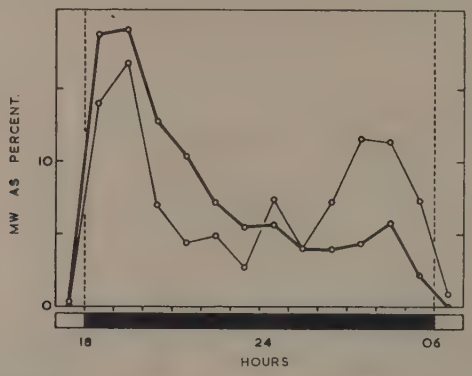

Fig. 2.—Flight activity curves for all species of mosquito ; all levels combined. Thick line—males ; thin line—females.

Traps were painted outside with black "Duco" and inside with aluminium paint. Each trap was held on to a collecting receptacle by four rubber strands attached to the platform. For the first two catches, material was collected direct into a one-litre beaker containing about 200 ml. alcohol (*ca.* 70 per cent.) (Corbet and Tjønneland, 1955), but this method proved to be unsatisfactory in two respects : the containers with fluid were awkward to handle on the tower, and the mosquitoes collected in alcohol were exceptionally difficult to identify. Subsequently, therefore, material was collected dry. A small funnel beneath each trap was made to fit snugly into a 250 ml. polythene screw-top jar, inside which was a double thickness of filter paper (16 by $2\frac{1}{2}$ inches) rolled to form a cylinder which fitted against the sides of the jar. This paper was impregnated with about one ml. trichloroethylene ("Trilene") a few minutes before being used, and remained potent for at least the next hour. Such an amount proved sufficient to immobilise even large moths. Altogether about 75 ml. Trilene were required for a single catch. Jars were closed immediately after collection, and remained so until the catch was examined, when the contents of each were spread out in a white enamel developing-tray, and the mosquitoes and tabanids removed.

Table II.—*Light-trap catches of mosquitoes according to genera*

	Males	Females	Totals (as percentage)
Anopheles . . .	3	.	0·1
Uranotaenia . .	51	29	4·1
Ficalbia . . .	19	25	2·3
Mansonia . . .	1133	186	67·6
Aedes . . .	52	5	2·9
Culex . . .	390	58	23·0
Totals . .	1648	303	100·0

The measure of central tendency used to record the average hourly catch is the Williams' mean (M_w) (*see* Part I, p. 253), usually expressed here on a percentage basis (*see* Haddow, 1960). Data are sufficient to indicate patterns of flight activity in relatively few species. For the remainder, therefore, generic or sub-generic groupings have been employed, account having been taken of the feeding habits of the females as indicators of ecological similarity. Thus, in the genus *Mansonia*, the bird-biting species (*see* Williams, Weitz and McClelland, 1958) have been grouped apart from the rest, which include *M. fuscopennata* and *M. uniformis*. The series of catches was too short for the precise effects of moonlight on the numbers taken to be determined (*see* Horsfall, 1943). However, hourly records of moon exposure were kept and are sufficient to show that the gross patterns of flight activity observed cannot be explained in this way.

The raw data on which the analyses are based will be deposited in the archives of the British Museum (Natural History), London.

Results

The results for mosquitoes and tabanids will be described separately. The full names of the species are given in Appendix A of Part I of this series.

Mosquitoes

The species and numbers caught at each level are given in Table I. The species recorded as *Uranotaenia* sp. nr. *pallidocephala* can be distinguished from *U. pallidocephala* sensu stricto only on tibial characters of the male. Thus the status of *U. pallidocephala* females in this series remains uncertain. Species of *Ficalbia* and *Culex* were not determined in all catches, and in certain *Culex* species only males were identified. In Table I, the presence only of such mosquitoes has been indicated (by a cross), since totals from them would not be comparable with the rest.

Two respects in which these catches differ from others made at the same site with human bait (Part VII, p. 316) is that the number of species represented is almost twice as great, and that the Index of Diversity (Fisher, Corbet and Williams, 1943) of the population sampled has a much higher value. This confirms that light-traps provide a relatively unselective method for sampling nocturnally active mosquitoes.

The catches consist mainly of several species of *Mansonia*, and of *C. insignis*. Determinations of the latter species were based on the examination of a long series of male terminalia from the early collections, in which this was the only species of the *C.* (*Neoculex*) *rima* Theo. group ; it was assumed thereafter that all adults of

Table III.—*Light-trap catches of mosquitoes at different levels*

Species or genus	Mean catch (M_w) expressed as percentage: Males Levels (feet) 120	90	60	30	G.L.	Females Levels (feet) 120	90	60	30	G.L.
Uranotaenia pallidocephala	.	.	.	.	.	35·1	13·0	6·5	19·5	26·0
U. nigromaculata	.	17·4	30·4	41·3	10·9	.	.	.	.	.
Uranotaenia spp.	4·2	13·6	26·3	40·7	15·3	38·1	9·7	19·4	14·9	17·9
Mansonia metallica	9·1	28·7	34·8	19·8	7·6	15·6	25·9	17·9	36·8	3·8
M. versicolor	28·2	28·2	22·5	14·1	7·0	.	.	.	.	.
M. pseudoconopas	2·5	14·2	33·4	27·9	22·0	9·4	24·5	28·3	28·3	9·4
M. maculipennis	7·8	25·6	27·9	22·6	15·9	.	.	.	.	.
M. fuscopennata	35·8	24·6	17·2	9·6	12·8	26·3	9·8	17·2	18·9	27·9
M. fraseri	19·7	29·2	27·4	14·9	8·8	23·6	34·5	32·7	9·1	.
Mansonia, bird-biting gp.	11·7	25·3	33·4	20·2	9·4	16·8	29·7	20·9	28·3	4·3
Aedes ingrami	.	11·6	18·6	23·3	46·5	.	.	.	.	.
Aedimorphus spp.	16·7	8·3	25·0	25·0	25·0	.	.	.	.	.
Neomelaniconion spp.	9·7	36·9	23·3	15·5	14·6	.	.	.	.	.
Culex insignis	0·9	16·5	28·8	25·1	28·7	10·5	30·8	29·1	19·2	10·5

this group caught in light-traps belonged to *C. insignis*. The validity of the determinations of that species therefore rests on the correctness of this assumption. In the genera *Uranotaenia* and *Ficalbia*, adults of which are seldom collected by other means, the catches reveal considerable nocturnal activity.

Males comprised 84·5 per cent. of the total mosquitoes caught, and predominated in all genera except *Ficalbia* (Table II).

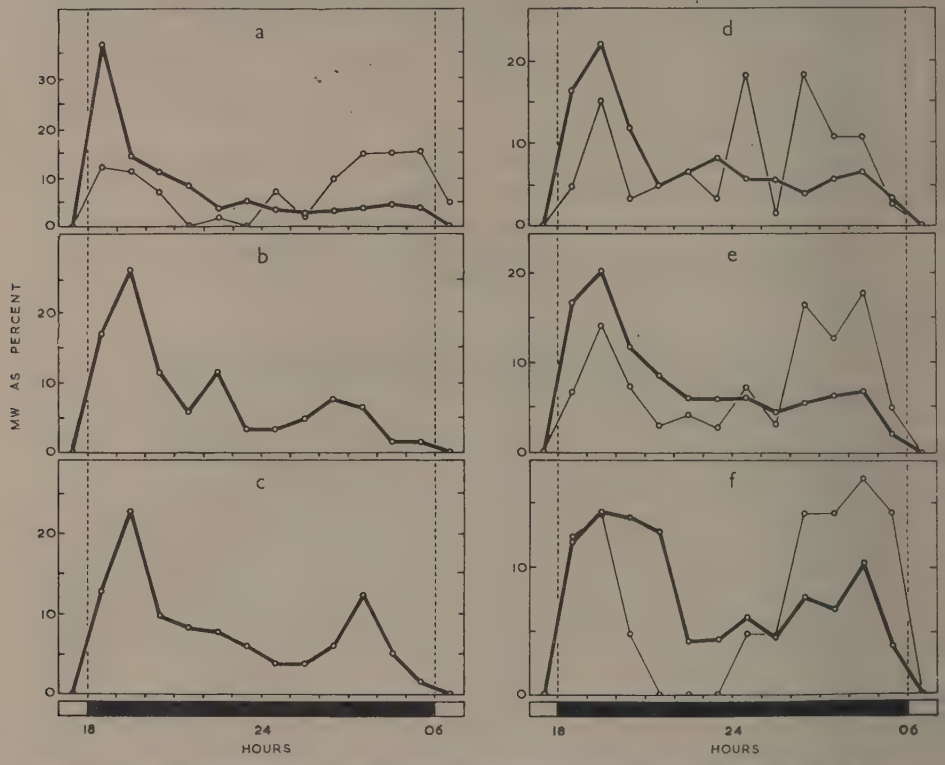

FIG. 3.—Flight activity curves for male and female *Mansonia* species; all levels combined. Thick lines—males; thin lines—females. *a*, *M. fuscopennata*; *b*, *M. maculipennis* (males only); *c*, *M. pseudoconopas* (males only); *d*, *M. metallica*; *e*, bird-biting *Mansonia* spp. (*i.e.* all except *M. fuscopennata* and *M. uniformis*); *f*, *M. fraseri*.

To facilitate comparison, the highest mean values for males have been adjusted to the same height (*cf.* Part VII, p. 316).

Table III shows the distribution according to level of those species or genera for which records were extensive enough to warrant analysis. The values given refer to the whole 14-hour period. These results confirm that light-traps can catch selectively according to level, and show that on the whole the commoner species (mainly bird-biting *Mansonia* species) are most active in and just above the canopy. As far as the data go, they indicate no consistent difference in vertical distribution between males and females, except possibly in *M. fuscopennata*, of which males are most active at 120 feet, whereas females are almost equally common at both ground level and 120 feet.

With regard to the general temporal distribution of flight activity, it may be said that in nearly all species there is a certain amount of activity throughout the night, but that there is a tendency for it to occur in two main waves—one between 18 and 22 hours (usually with a peak at 19-20 hours), and another between 02 and

06 hours (with a less well-defined peak at 03–05 hours). There is thus a period near, or shortly after, midnight when activity is at a low level. This is well illustrated by the combined catches for all species of mosquito (fig. 2).

When describing patterns of flight activity in detail, it will be necessary to consider species or genera separately according to sex and level. The composition of the catches makes it inevitable that most attention will be given to species of *Uranotaenia* and *Mansonia*, and to *C. insignis*.

In general, males and females show different patterns of activity (fig. 2). In *Mansonia* (fig. 3) and *Culex* (fig. 4), males are more active during the first part of the night, and females during the second, a phenomenon noted previously in *M. fuscopennata* (Corbet and Haddow, 1961). In *Uranotaenia*, however, the two sexes show broadly similar patterns of flight activity, except that only males (mainly *U. nigromaculata*) are represented in the second wave (fig. 4).

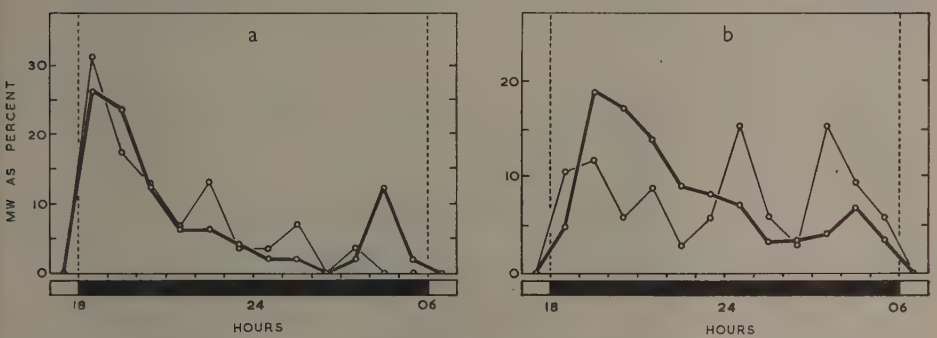

Fig. 4.—Flight activity curves for male and female mosquitoes ; all levels combined. Thick lines—males ; thin lines—females. *a*, *Uranotaenia* spp. ; *b*, *C. insignis*. Ordinates adjusted as in figure 3.

Data for four species (*U. nigromaculata*, *M. pseudoconopas*, *M. maculipennis*, and *Aedes ingrami*) and for the subgenus *Neomelaniconion* are sufficient to indicate patterns of flight activity only in males (figs. 3*b*, *c* and 5). The activity pattern for *M. pseudoconopas* and *M. maculipennis* resembles that for males of the other bird-biting species of *Mansonia* (figs. 3*d*, *e* and *f*), and it is therefore probable that the pattern for females is also similar.

Until now, the flight activity patterns which have been described have been based on results for all levels combined. Such a presentation is considered to be meaningful since, in most cases, a species is active throughout the night at all levels sampled. Nevertheless, in some species, patterns of activity at upper levels differ slightly, but consistently, from those at lower levels.

At 120 feet, light-trap catches of males of *Mansonia* species are greatest at 18–19 hours (figs. 6 and 7*a*), whereas at lower levels they are usually greatest from one to two hours later. This progressively later incidence of the first activity wave at lower levels is well shown in *M. fraseri* (fig. 7*a*), but can be discerned in other species also, including *M. metallica*, for which data are not included here. *C. insignis* (fig. 7*b*) differs from the *Mansonia* species in that the second wave of male activity is apparently confined to higher levels.

Data for females are insufficient to show whether or not marked differences in activity occur according to level ; but in *M. fuscopennata* (fig. 8*a*), and in the combined sample of bird-biting *Mansonia* species (fig. 8*b*), trends appear which are broadly similar to those encountered in the males (figs. 6 and 7), the activity waves being better defined at higher levels.

Thus catches in light-traps provide evidence that *M. fuscopennata* and bird-biting species of *Mansonia* carry out vertical movements during the night, such that both sexes are most prevalent above the forest canopy in the hour after sunset, but that the centre of activity subsequently moves downwards—into the canopy and below it—and does not rise again until one to three hours before sunrise.

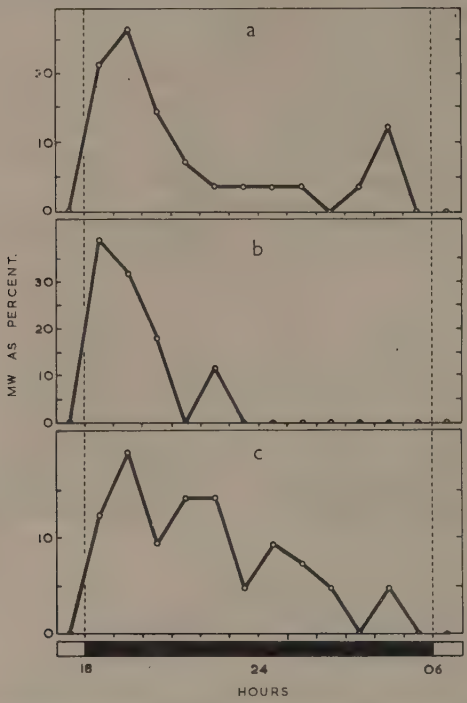

FIG. 5.—Flight activity curves for male mosquitoes ; all levels combined. *a*, *U. nigromaculata* ; *b*, *Ae. ingrami* ; *c*, *Neomelaniconion* spp. Ordinates adjusted as in figure 3.

Tabanids

The species and numbers caught at each level are given in Table IV. As might be expected, the number of species is greater than that in human-baited catches at the same site (Part VII), and includes *Thaumastocera cervaria*, adults of which are thought not to suck blood (Oldroyd, 1954).

Males comprised about 76 per cent. of the total specimens collected, and were taken only in traps above the canopy. Females were caught mainly in and below the canopy.

Males and females differ in their patterns of flight activity (fig. 9), a phenomenon noted also in *Tabanus thoracinus* outside forest (Haddow and Corbet, 1960). At Mpanga, males showed activity throughout the night with a marked peak during the hour before sunrise, whereas females were active mainly in the first three hours after sunset.

A few tabanids (not included in Table IV or fig. 9) were also caught at mercury-vapour light in the first two catches (*H. ugandae*, during the hours 09–10 and 16–17), or at yellow light at night at the camp on the forest edge (*H. fusca* and *H. patellicorne*). All were females. It is perhaps also of interest to record that three female *Tabanocella perpulcra* were apparently attracted to the generator when it was operating in the late afternoon.

Discussion

These data have been sufficient to indicate that recurrent patterns of nocturnal flight activity exist in certain sylvan mosquitoes and tabanids. Considerable activity above the forest canopy has been noted, particularly of males, and the times of night at which it is greatest suggest that it may be connected with the patterns of swarming shown by these two groups (Part V, p. 284). In some species, the females of which bite at a restricted time and level, the males may be active from ground level to well above the canopy at night. Apparently, therefore, it cannot be assumed that a mosquito which is diurnal in one sex is necessarily so in the other, and when interpreting light-trap catches it must constantly be remembered that the phototactic responses of males and females may differ significantly (*see* Pratt, 1944). It is nevertheless interesting to observe that, with the exception of *Ae. apicoargenteus* and *Ae. leptolabis*, the genus *Aedes* was represented only by males, these being mainly of species which bite by day in forest (Haddow, 1960 and Part VII). This draws attention to the possible value of light-traps in taxonomic studies of subgenera such as *Aedimorphus* and *Neomelaniconion*, in which specific determinations often depend on males (*see* Blanton *et al.*, 1955).

These catches have shown that in certain species of mosquitoes, particularly of the genus *Mansonia*, nocturnal flight activity is manifest in two broad waves, of which the peaks fall most often at 19–20 hours and 03–05 hours, respectively. This pattern differs from other biphasic flight patterns revealed by light-trap studies

Table IV.—*Light-trap catches of tabanids according to time and level*

	Males								Females						
	Haematopota fusca	*H. patellicorne*	*H. ugandae*	*H. lamborni*	*Thaumastocera cervaria*	*Tabanus thoracinus*	*Chrysops centurionis*	Totals	*H. ugandae*	*T. cervaria*	*Tabanus secedens*	*T. thoracinus*	*C. centurionis*	*Tabanocella perpulcra*	Totals
Hour															
17–18	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1
18–19	.	.	.	.	.	.	1	1	.	.	1	.	1	.	2
19–20	.	.	.	.	1	1	2	4	1	1	.	1	1	.	4
20–21	.	.	1	.	1	.	.	2	1	1	.	.	.	1	3
21–22	1	.	.	.	.	.	.	1	.	.	.	.	.	.	.
22–23	1	.	.	.	1	.	.	2	.	1	.	.	.	.	1
23–24	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.
00–01	.	.	.	.	1	.	1	2	.	.	.	.	.	.	.
01–02	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1
02–03	2	.	.	.	.	.	.	2	.	.	.	.	.	.	.
03–04	.	.	.	.	.	1	2	3	.	.	.	.	.	1	1
04–05	.	.	.	.	.	2	3	5	.	.	.	.	.	1	1
05–06	1	2	3	.	.	7	8	21	.	.	.	.	.	.	.
06–07	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.
Totals	5	2	4	1	4	12	17	45	4	3	1	1	2	3	14
Levels (feet)	All hours combined								All hours combined						
120	2	2	4	.	2	7	11	28	.	.	.	1	.	1	2
90	3	.	.	1	2	5	6	17	.	1	.	.	1	.	2
60	.	.	.	.	.	.	.	.	.	2	1	.	.	1	4
30	.	.	.	.	.	.	.	.	2	.	.	.	.	1	3
G.L.	.	.	.	.	.	.	.	.	2	.	.	.	1	.	3

(Chironomidae : Williams, 1935 ; Trichoptera : Corbet and Tjønneland, 1955 ; Ephemeroptera : Tjønneland, 1960), in that the peaks of activity are not associated so closely with sunset and sunrise. In this respect it differs also from the patterns of other types of mosquito activity at Mpanga (Parts V and VII). This being so, it is important at this stage to consider carefully what it is that light-trap catches

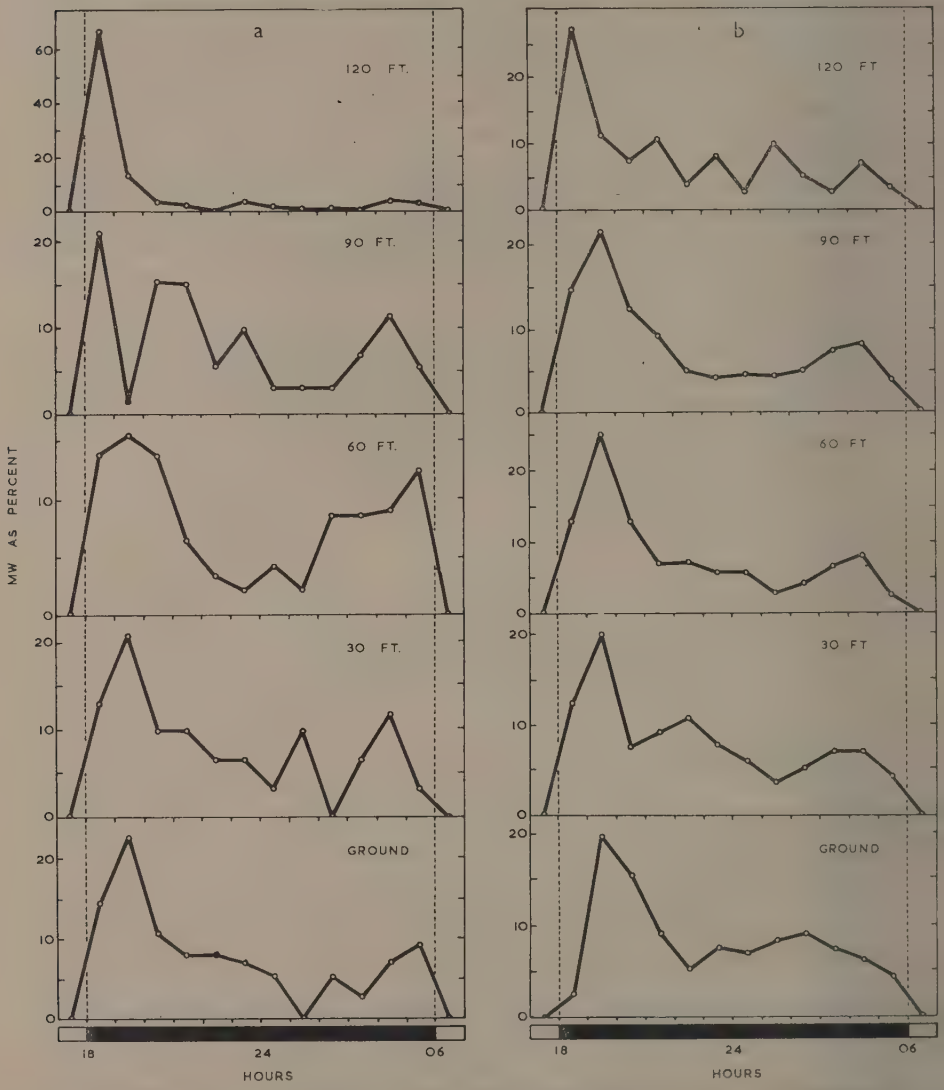

FIG. 6.—Flight activity curves for male *Mansonia* species at five levels. *a*, *M*, *fuscopennata* ; *b*, bird-biting *Mansonia* spp. Ordinates adjusted as in figure 3.

actually show. It has often been stressed (*e.g.* Williams, 1935) that the numbers of insects caught in light-traps represent a resultant of three factors : abundance, activity, and level of phototactic response. In presenting the Mpanga results so far, it has been assumed that successive changes in mean hourly catch reflect corresponding changes in activity—that is, that short-term variations in abundance

and phototactic response have not determined the trends observed. With the noteworthy exception of studies designed to assess the effects of moonlight on activity (*e.g.* Williams, 1936 ; Horsfall, 1943), this assumption is usually made when interpreting light-trap data. Certain observations made at Mpanga, however, have indicated that it is not always justified to assume that the phototactic response, at least, may not undergo short-term fluctuations.

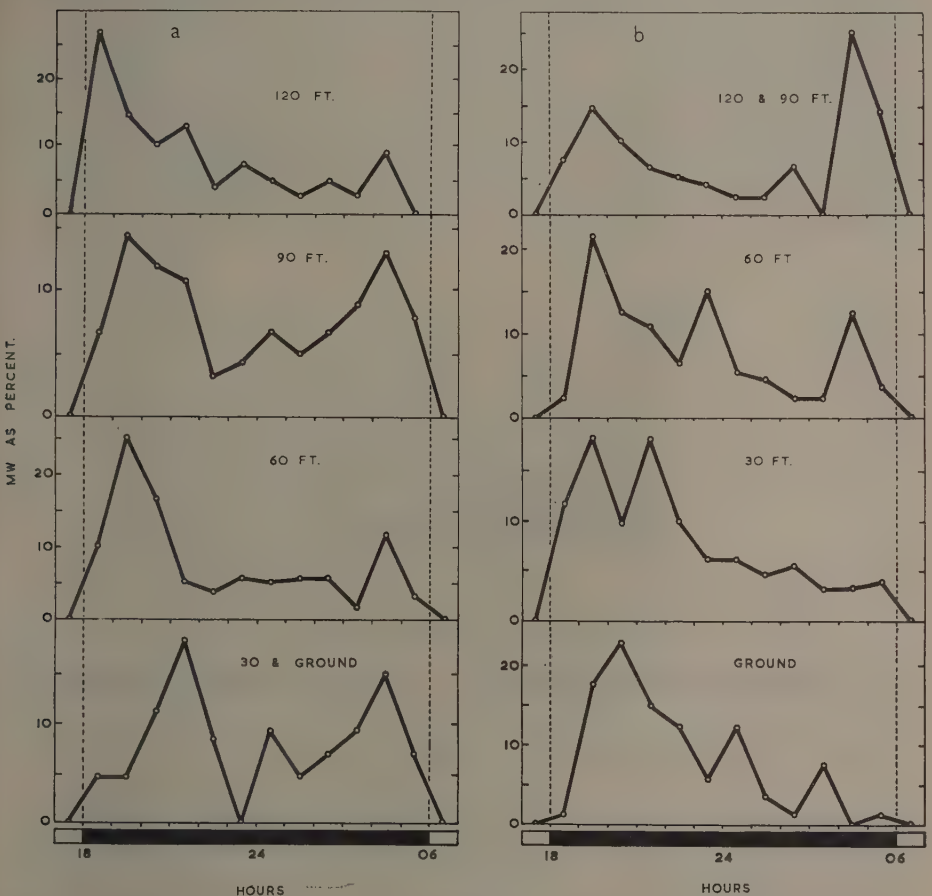

FIG. 7.—Flight activity curves for male mosquitoes at different levels. *a*, *M. fraseri* (lowest two levels combined) ; *b*, *C. insignis* (highest two levels combined). Ordinates adjusted as in figures 3.

On the tower at Mpanga, male *M. fuscopennata* swarm regularly above the top platform during the period 1815 to 1855 hours (Part V, p. 292). Although certain mosquitoes are known to be very easily dispersed by light when swarming (*e.g.* Nielsen and Nielsen, 1953), these swarms of *M. fuscopennata* appeared to form in exactly the same way whether or not a light-trap was in operation at 120 feet. The design of the light-trap (fig. 1) was such that males swarming in their usual position (four feet or more above the platform) would have been illuminated but unable to see the light-source itself. On one occasion, however, a Robinson-trap without a roof was run on the top platform from 17 to 07 hours. It was then noticed that male *M. fuscopennata* still formed swarms as usual, and furthermore that they maintained

them in full view of the bulb, and sometimes as little as two feet away from it. A likely explanation for this phenomenon is that, while males are engaged in swarming, their phototactic response is significantly reduced. Comparison of activity curves for biting and flight in female *M. fuscopennata* supports this idea, for catches in light-traps at 60, 90 and 120 feet, just before sunrise, are falling off at a time when biting activity there is increasing (Part VII, p. 324). A similar phenomenon has been recorded in ground level catches of this mosquito at Entebbe (Corbet and Haddow, 1961), while Breev (1958) has reported that in temperate latitudes mass flights of mosquitoes to light begin about an hour after the evening peak of biting activity.

Interpreted in this way, these observations lead to the conclusion that light-traps will attract those phototactic mosquitoes which are flying at night, but only at times when they are not preoccupied with some other specific activity (*e.g.* swarming, biting or oviposition). The fact that peak catches of male mosquitoes (*Mansonia* spp.) at 120 feet fell in the same hour that they swarmed there, does not necessarily conflict with this hypothesis. Swarming of all species recorded ceased at between

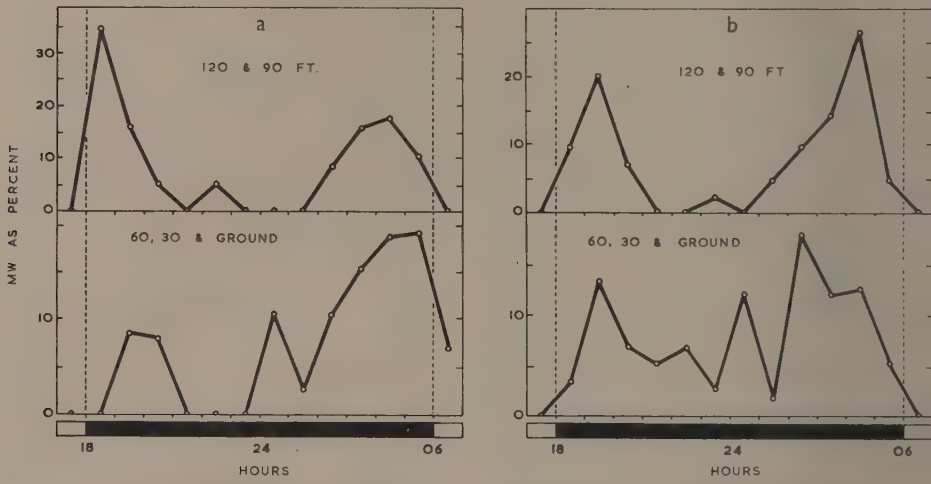

FIG. 8.—Flight activity curves for female *Mansonia* species above and below the canopy. *a*, *M. fuscopennata* ; *b*, bird-biting *Mansonia* spp. Ordinates adjusted as in figure 3.

1820 and 1850 hours, at a modal time of 1835–1840 (Part V, p. 290), and if at this time males became phototactic again, it might be expected that they would be caught in the nearest light-trap. It is noteworthy that rapid changes in phototactic response, of an order such as this, have been recorded in Ephemeroptera by Kennedy (1925) and by Edmunds, Nielsen and Larsen (1956). A careful comparison of catches made with sweep-nets and light-traps would doubtless provide useful information on this point.

That light-traps are principally recording non-specific locomotor activity is indicated by evidence of another kind. In seven catches, the gonotrophic stage of all female *Mansonia* was recorded. The results show that the great majority (94·4 per cent.) of the 126 females examined were unfed and did not contain visible eggs. They must therefore have been caught in that limited phase of adult life which lies between either emergence or oviposition, and the acquisition of a blood meal. The absence of gravid females shows that none was caught while seeking an oviposition site, while the pattern of the biting-cycle (Haddow, 1956*a*, Part VII and *unpublished*) shows that they were not experiencing the immediate urge to bite. On the contrary, we have seen (fig. 8) that, after midnight, female *M. fuscopennata* are flying above

the canopy from 02 hours onwards, yet in the morning they begin to bite intensely there only between 05 and 06 hours. Thus a wave of non-specific locomotor activity is apparently responsible for bringing the females to a site where they will later seek a host. If this interpretation of the data is correct, it necessitates modification of the earlier suggestion (Mattingly, 1949*b*) that the biting-cycle may represent the frequency with which a population in random flight comes within the range of attraction of the host. An additional qualification must now be introduced, namely, that the mosquitoes also must possess the urge to bite.

Having attempted to define the kind of information which light-traps can be expected to provide, we can briefly discuss the biological significance of the findings.

It may be said at once that the waves of activity observed occur at times when changes in the physical environment are extremely slight (Part II, p. 257), and it is therefore very unlikely that microclimatic factors provide the proximal stimuli which position these waves. Another possibility which should be examined is that,

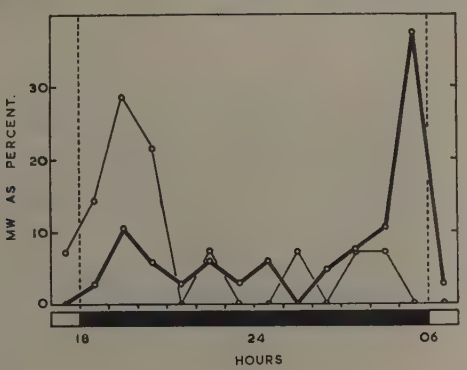

Fig. 9.—Flight activity curves for all species of tabanid; all levels combined. Thick line—males; thin line—females.

as suggested by Lumsden (1952), the observed pattern is the result of staggered activity in mosquitoes of different ages. This question will be discussed at greater length elsewhere (Part VIII), but for the moment it will suffice to say that, in the species of *Mansonia* obtained in these catches and examined by me, the overall activity curves could not be explained in this way.

It may be concluded then that the waves of nocturnal activity which have been observed are probably manifestations of an endogenous rhythm which apparently persists throughout a significant part of adult life. It will be appropriate to consider some implications of this finding in the light of Mattingly's earlier suggestion (1949*b*) that intrinsic rhythms may play a large part in the overt manifestations of cyclical behaviour, such as biting, which are encountered in field studies of mosquitoes.

Recent work has shown that in *Aedes aegypti* oviposition activity is cyclical (Haddow and Gillett, 1957), but only when its temporal position in the diel has been determined by the appropriate stimulus, which happens to be a change from light to dark (Gillett, Corbet, and Haddow, *in press*). Once positioned in this way, oviposition remains cyclical even under constant conditions (Haddow, Gillett and Corbet, 1961). In such a case, it would clearly be inappropriate to look for current microclimatic changes which could determine the pattern of the oviposition cycle.

The persistence of acquired endogenous rhythms of this kind needs to be especially considered when interpreting cyclical activities in insects with relatively long-lived adults. Those cyclical activities which are poorly synchronised, and which occur

when environmental changes are very small, must be regarded as likely to have a strong endogenous component. On the other hand, the timing of well-synchronised cyclical activities, such as swarming, which take place when environmental changes are rapid, is more likely to be determined by critical responses to extrinsic factors. This view is strongly supported by the results of Provost (1958) who recorded an exceptional temporal extension of swarming in *Psorophora confinnis* only on a night when moonlight postponed the usual fall of darkness.

The observations quoted above are consistent with the view that in mosquitoes the cyclical activities which compose the daily programme of adult life are controlled by an interplay of both endogenous and exogenous rhythms (Gillett, Haddow and Corbet, 1959). A broad, largely endogenous, rhythm may be manifest in one or more waves of poorly synchronised activity, usually occurring at times in the diel when environmental changes are small or variable. As examples of rhythms of this kind may be cited the non-specific flight activity of *Mansonia* spp., the biting of *Ae. aegypti* (Lumsden, 1957 ; McClelland, 1959), or the oviposition activity of *M. fuscopennata* (Haddow and Gillett, 1958) or of *Ae. aegypti* (Haddow and Gillett, 1957).

Superimposed, as it were, upon this endogenous foundation, are certain well-synchronised activities which are probably mainly exogenous, and which typically occur near sunset or sunrise, when environmental changes are sufficiently rapid to provide critical stimuli. Biting in *Ae. africanus* and in the tabanid, *Chrysops centurionis* (Haddow, Gillett, Mahaffy and Highton, 1950), and swarming in male *Mansonia* spp. (Part V, p. 292) are probably examples of this kind of rhythm.

Acknowledgments

I wish to thank Dr. A. J. Haddow for helpful suggestions during this work, particularly with regard to the design of the light-trap ; Mr. Y. Senkubuge for his valued assistance in the field ; and Mrs. E. C. C. van Someren and Mr. H. Oldroyd for help with the identification of certain mosquitoes and tabanids, respectively.

Summary

1. Fifteen all-night catches with mercury-vapour light-traps were made at five levels on a tower in Mpanga Forest, Uganda. Each trap was emptied hourly, and the Culicidae and Tabanidae which had been caught were identified and counted.

2. The light-traps sampled a more diverse mosquito population than did catches using human-bait at the same site.

3. Males comprised 84·5 per cent. of the 1951 mosquitoes caught, and about 76 per cent. of the 59 tabanids.

4. Mosquitoes most commonly encountered were species of *Uranotaenia*, *Mansonia* and *Culex*. Within a species, activity varied according to level, but males and females usually showed a similar vertical distribution. Nocturnal flight activity, as indicated by the light-trap catches, was cyclical, and usually occurred in two broad waves, males predominating in the first and females in the second. At higher levels, the peak of male activity usually occurred earlier, and the pattern of female activity tended to be better defined. Thus the catches provided evidence for vertical movements.

5. In tabanids there were well-defined differences between males and females : males were only caught above the canopy, and females mainly below it ; males flew mainly in the hour before sunrise, and females in the second hour after sunset.

6. It is suggested that light-traps only sample mosquitoes engaged in non-specific flight activity, and that for this reason the flight patterns they reveal are unlikely to correspond to those of more specific activities such as biting.

7. It is suggested that the rhythmic flight activity recorded in this work has a strong endogenous component. The interplay of endogenous and exogenous rhythms in daily cyclical activity of mosquitoes is briefly discussed.

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

VII. THE BITING BEHAVIOUR OF MOSQUITOES AND TABANIDS

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The Mpanga Forest and the high steel tower on which this work was carried out have been described in Part I of this series, where also are given the full scientific names of all species of biting Diptera taken; abbreviated names will accordingly be used below. The measure of central tendency here employed is the logarithmic transformation introduced by Williams (1937), which has also been discussed more fully in Part I, p. 253.

In the present communication a description is given of the results obtained in a series of forty 24-hour catches of mosquitoes coming to bite man, carried out at weekly intervals between September 1958 and June 1959. These catches were made simultaneously at 120, 90, 60 and 30 feet and at ground level. The bait at each level consisted of two Africans. The writer considers larger groups to be preferable, but in the interests of economy the numbers had to be kept to the lowest possible level. The methods used in this and other series of 24-hour catches have been discussed in detail in another paper (Haddow, 1954), to which reference should be made for detail. For the present purpose it is enough to note that the insects coming to bite were grouped by hour and by level, and that sunset, 1800 hours " catch-time " (*see* Part I, p. 253), was the key point of reference.

At the outset it may be stated that at Mpanga the yield of tree-hole breeders was very poor, except in the case of *Aedes apicoargenteus*. Larvae seemed abundant enough in tree-holes and in trap bamboo containers (Part IV, p. 275), but the adults were unaccountably scarce. Preliminary work at ground level showed all the important species to be present, and it was concluded that, as usual, they would be found at their preferred levels in greater numbers. Yet in the case of *Ae. africanus*, normally the dominant canopy species in Uganda lowland forest, only 16 were taken in the entire series, whereas in a reasonably favourable locality three times this number may be taken on a canopy platform in a single evening. Of over 40 Uganda forests so far studied, Mpanga is the first to be found in which *Ae. africanus* was not prevalent in the canopy, if certain mountain forests (which lie above its altitude limit) be excepted.

Members of the Institute staff who work on mosquitoes are becoming increasingly interested in the vertical distribution of mosquitoes in forest as a dynamic rather than a static feature of behaviour. As interest is increasing with regard to birds and arboreal mammals as wild hosts of virus disease transmissible to man, the links between the forest floor and the canopy must be acknowledged as of major importance. The occurrence of daily vertical movements was first pointed out—in *Ae. africanus*—by Mattingly (1949*a*) and has been confirmed by the writer (1954), who also recorded such movements in *Ae. ingrami*, *Mansonia pseudoconopas*, *M. fuscopennata* and *M. aurites*. One of the objects of making studies on a high tower was to investigate these vertical movements in greater detail and to find whether or not they extended to the zone above the canopy.

The vertical distribution of all species taken in the 40 catches here discussed is given in Table I, and in figure 1 " kite diagrams " have been used to show the distribution of some of the more important species.

In the construction of graphs and diagrams it is often simplest, when comparing species or levels, to reduce the figures to percentages. There are, however, certain disadvantages inherent in this method. Thus in a small sample the presence or absence of a very few specimens may cause an apparently dramatic rise or fall in the level for a given hour. Similarly, where activity at a given level is prolonged over a considerable period, the graph will tend to be flat and uninteresting when compared with one from a level where activity has been restricted in duration, and a first inspection of such graphs may give the reverse impression of a level that is actually

TABLE I.—*The vertical distribution of biting mosquitoes, Mpanga Forest.* (*T = total; M_w = Williams' mean, which has been multiplied by* 1000, *except in the case of* M. fuscopennata, *where it has been multiplied by* 100.)

Species		Level (feet) 120	90	60	30	G.L.
Anopheles obscurus	(T)	.	.	.	.	1
A. implexus	(T)	.	.	.	.	10
A. gambiae	(T)	.	.	1	.	.
Hodgesia cyptopus	(T)	.	2	3	2	12
Mansonia pseudoconopas	(T)	.	1	.	3	2
M. maculipennis	(T)	.	.	1	1	.
M. fuscopennata	(T)	2256	2775	907	601	4731
	(M_w)	(4193)	(5226)	(1519)	(1085)	(8823)
M. aurites	(T)	26	3	2	4	.
M. fraseri	(T)	3	3	.	1	.
M. africana	(T)	4	7	2	.	5
M. uniformis	(T)	1	1	.	.	.
Aedes grahamii	(T)	2	.	2	.	.
Ae. longipalpis	(T)	.	.	11	2	.
Ae. ingrami	(T)	.	2	2	16	3
Ae. apicoargenteus	(T)	9	68	385	495	144
	(M_w)	(144)	(942)	(4309)	(6903)	(2629)
Ae. dendrophilus	(T)	.	.	.	.	1
Ae. africanus	(T)	1	7	2	2	4
Ae. domesticus group	(T)	.	.	.	.	3
Ae. tarsalis group	(T)	.	.	.	.	39
Ae. cumminsii	(T)	.	.	.	.	3
Eretmapodites semisimplicipes	(T)	.	.	3	2	1
E. hightoni	(T)	.	.	.	.	2
Culex tigripes	(T)	1	.	.	.	3
C. poicilipes	(T)	.	1	.	.	.
C. annulioris	(T)	1	.	3	7	119
	(M_w)	(17)	(.)	(53)	(128)	(888)
Culex spp. indet.	(T)	.	3	6	2	4
Haematopota ugandae	(T)	.	.	.	.	6
Chrysops centurionis	(T)	1	.	4	.	.

the most highly favoured. An example of this undesirable effect will be found in a figure showing the biting-cycle of *Anopheles gambiae* in the Semliki Forest (Haddow, 1954). Here the graph which commands most attention is that for the canopy, where this species was relatively scarce, while the least impressive is that for ground level, where it was present in enormous numbers. On the other hand, the yield from different levels may vary so greatly that a comparison on a straight arithmetic basis is not feasible graphically, while the use of a logarithmic scale once more favours the small, as opposed to the large, sample.

An attempt has been made to overcome some of these difficulties by adjusting the scale of each graph individually. Thus, where five levels are compared as, for example, in figure 2, the greatest ordinate is of the same height in each case. Simi-

larly, in the vertical distribution diagrams, the scale is adjusted so that each has the same maximum width. This method is more laborious than the others, but does seem to have much to recommend it. Where percentages are necessary to permit comparison of two areas in a single graph, the same principle has been adhered to, the greatest ordinates in successive graphs being of the same height, as in figure 7.

The results may now be discussed :

Anopheles implexus

This, the only species of *Anopheles* on which any comment can be made, was ground-haunting and diurnal in this area as at Entebbe. In Bwamba County in western Uganda, though still ground-haunting, it is essentially nocturnal (Haddow, 1954).

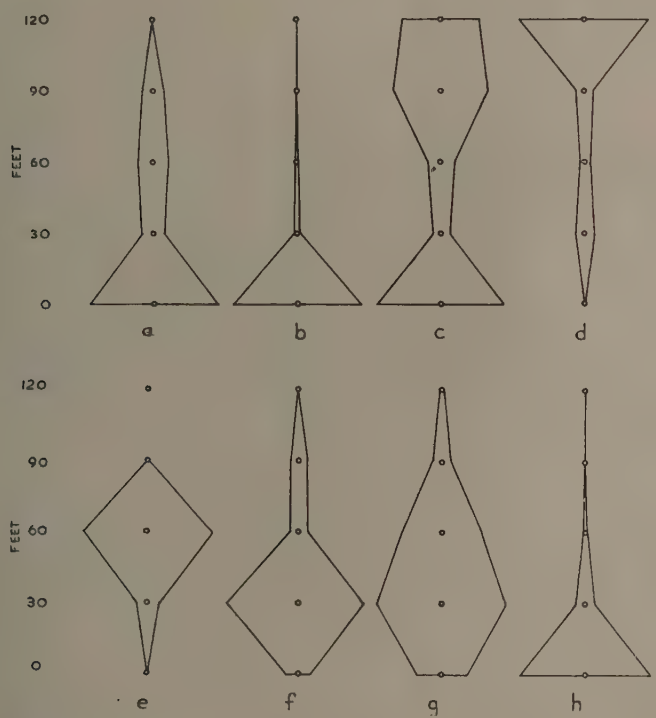


Fig. 1.—The vertical distribution of mosquitoes in Mpanga Forest. In the case of the scarcer species, which are marked by asterisks, arithmetic results have been given ; M_w is used in the others. The scales are adjusted so that the maximum width of all diagrams is the same. *a, H. cyptopus* ; b, M. fuscopennata* (diurnal distribution) *; c, M. fuscopennata* (nocturnal distribution) *; d, M. aurites ; e, Ae. longipalpis* ; f, Ae. ingrami* ; g, Ae. apicoargenteus ; h, Culex annulioris.*

Hodgesia cyptopus

This tiny mosquito is a vicious biter, active by day only. Its vertical distribution (Table I ; fig. 1,) was similar to that encountered in unpublished work at Zika, ground level being the preferred zone. At Zika the biting-cycle in forest is essentially biphasic. In the present series the main yield was around midday (Table II) but the total taken was too small to permit any firm conclusions to be drawn.

Mansonia fuscopennata

This was the most abundant mosquito at Mpanga, and the findings will therefore be discussed in some detail. *M. fuscopennata* is very widely known as a " nuisance mosquito " in East Africa, and it is in all probability involved in the transmission of the dangerous and economically important virus of Rift Valley fever, which affects both livestock and man. Thus Daubney and Hudson (1931), describing the first known epizootic, concluded that *M. fuscopennata* (which in this first paper they refer to as *Taeniorhynchus brevipalpis*) was probably an important vector and during their

TABLE II.—*The biting-cycles of some of the less abundant species.* (T = *total*, M_w = *Williams' mean, which has here been multiplied by* 1000.) *Some of these species were confined, or virtually confined, to a single level. In no case were numbers sufficiently large for analysis by separate levels.*

Hour beginning	*Anopheles implexus* (T)	*Hodgesia cyptopus* (T)	*Mansonia aurites* (T)	*Mansonia africana* (T)	*Aedes longipalpis* (T)	*Aedes ingrami* (T)	*Aedes africanus* (T)	*Aedes taeniatus* group (T)	*Culex annulioris* (T)	*Culex annulioris* (M_w)
06	.	3	.	1	.	.	.	2	2	(35)
07	.	.	.	.	.	.	.	2	3	(53)
08	.	.	.	.	1	.	.	10	1	(17)
09	.	2	.	.	2	.	.	3	1	(17)
10	.	.	.	.	.	.	.	.	1	(17)
11	2	4	.	.	3	1	.	.	.	.
12	1	5	.	.	.	.	1	.	.	.
13	1	1	.	.	3	.	.	2	.	.
14	1	.	.	.	1	1	.	2	1	(17)
15	1	2	.	.	2	2	.	1	.	.
16	1	1	.	.	1	3	.	5	1	(17)
17	2	1	.	.	.	11	6	7	14	(180)
18	.	.	20	5	.	3	6	3	69	(1300)
19	1	.	5	2	.	.	1	1	5	(109)
20	.	.	3	1	.	1	2	.	5	(109)
21	.	.	1	1	.	.	.	.	1	(17)
22	.	.	1	.	.	.	.	.	7	(120)
23	.	.	1	1	.	.	.	.	1	(17)
00	.	.	.	1	.	.	.	1	4	(53)
01	.	.	2	1	.	.	.	.	5	(90)
02	.	.	.	1	.	.	.	.	3	(53)
03	.	.	1	.	.	.	.	.	3	(53)
04	.	.	1	.	.	.	.	.	2	(35)
05	.	.	.	2	.	.	.	.	1	(17)

experiments they produced immunity to the virus in a lamb into which they had inoculated five wild-caught specimens, one at least of which must have been infected. During the past year *M. fuscopennata* has again been implicated in the epidemiology of this important infection, virus having been isolated from wild-caught specimens collected during an outbreak in the Entebbe area (Williams, Woodall, Corbet, and Haddow, 1960), together with a strain of another virus, so far unidentified.

Since the publication of the first series of 24-hour catches in Bwamba County (Haddow, 1945*a*) it has been known that even in forest the biting activity of this species is very largely nocturnal. In Bwamba, however, *M. fuscopennata* is not particularly common and, while the biting-cycle found in the canopy resembles that described below in many particulars, the cycle observed at ground level tends

to be very irregular. The description now given is, it is believed, the first detailed account of biting activity in this species based on a really large sample, though short notes have previously been published by the writer (1956*a*) and by Haddow and

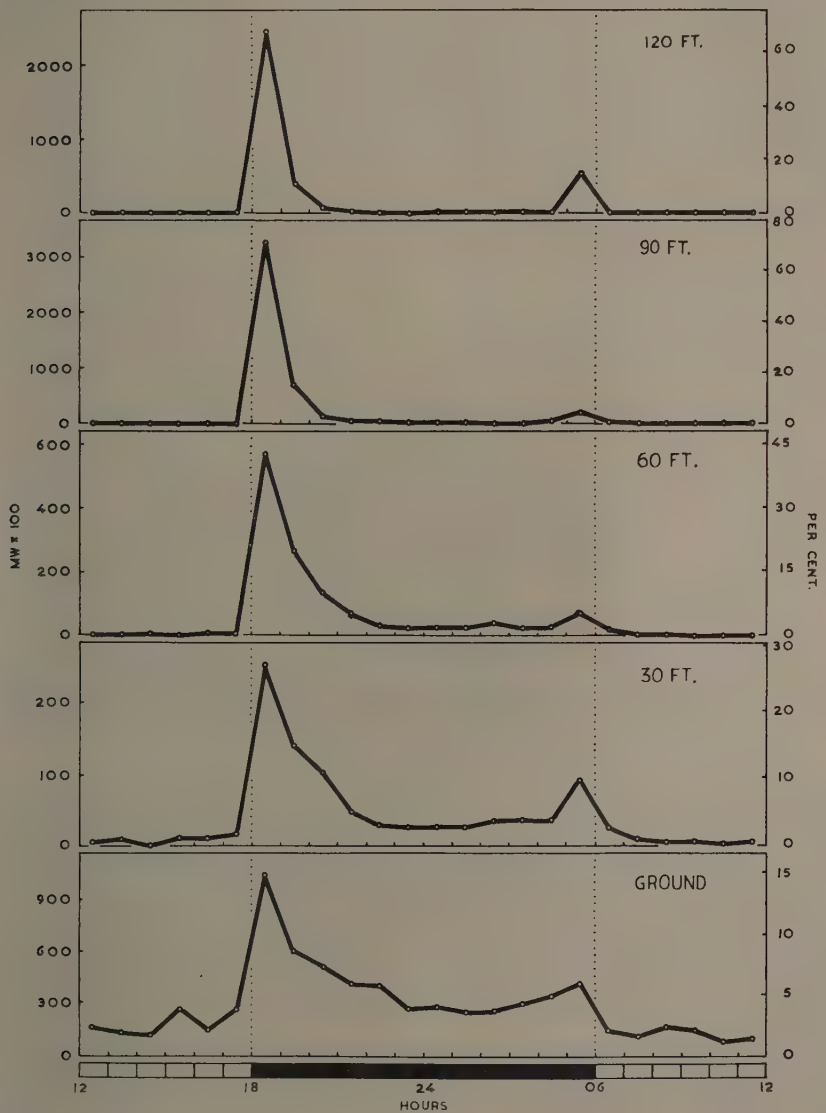


FIG. 2.—The biting-cycle of *M. fuscopennata* at Mpanga, by hour and level. The graphs show the results for 120 feet, 90 feet, 60 feet, 30 feet and ground level. The scales have been adjusted so that the greatest ordinate is of the same height in each case.

Gillett (1958). The biting-cycle, as seen at Mpanga, is shown in Table III and figure 2. It will be noted that at the highest level, 120 feet, there is a very sharp burst of biting activity in the hour after sunset, and a little in the succeeding hour. Thereafter there is virtually no further biting activity till the hour before sunrise when there

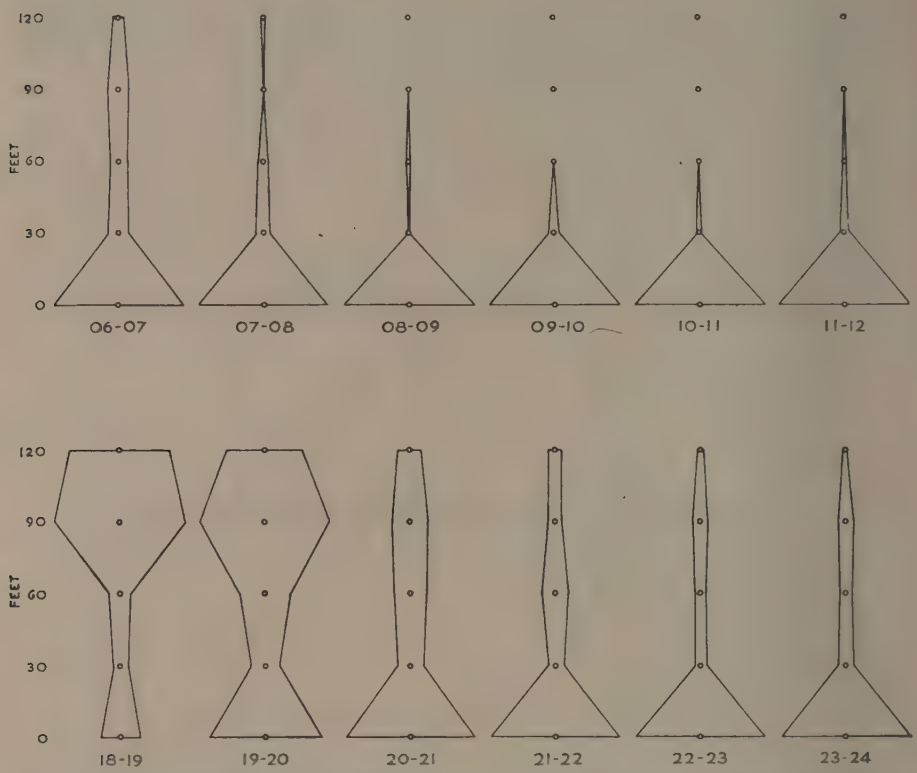
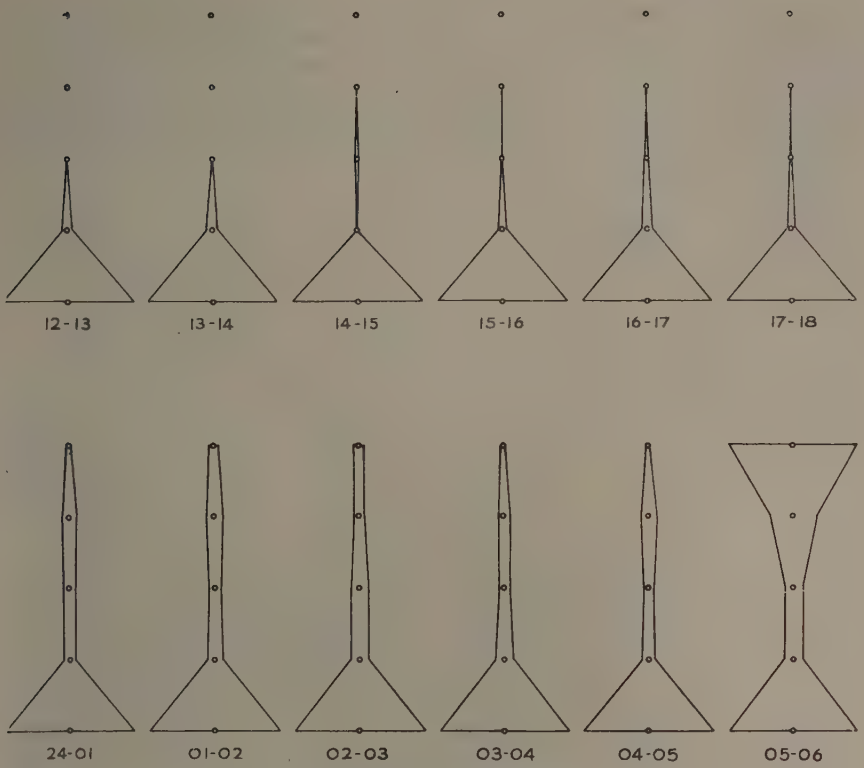


FIG. 3.—The vertical distribution of biting females of *M. fuscopennata* hour by hour. The upper row shows the daylight hours, and the lower row the hours of darkness. The scales have been adjusted so that the greatest width of the diagrams is the same in all cases.

is a small but well-marked peak. At all the lower levels these peaks are also apparent, but they become progressively less well-marked as ground level is approached while, on the other hand, the activity in the intervening hours of darkness progressively increases. Only at ground level is there any significant amount of biting by day and at the levels over 30 feet virtually no day biting occurs except in the hour after sunrise. The phenomenon just described of a biting-cycle showing very pronounced characteristics at the higher levels, which becomes progressively less well marked as ground level is approached, has already been demonstrated in *A. gambiae* (Haddow, 1954) and it may be mentioned that it occurs in various other species also.

The results just quoted show the importance of studying all levels before any conclusions are drawn concerning the biting-cycle of a given species. Thus a study of the upper levels only would in the present case have led to the conclusion that the form of the biting-cycle in *M. fuscopennata* depends on a simple photoperiodic response to crepuscular light. That this is not the case is shown by the results from ground level. Detailed studies, which will be discussed elsewhere, have shown that in the canopy the main wave of biting activity in this species begins when the light intensity has fallen to the neighbourhood of 0·5 foot-candles, and ends when it has dropped to about 0·002 f.c. At ground level, however, it continues—though with reduced vigour—throughout the day when, at its maximum, incident light on the forest floor may be as much as 300 f.c.



(*For legend see facing page*)

In the paper quoted (Haddow, 1954), it was mentioned that *M. fuscopennata* makes daily vertical migrations, and that it may be watched rising through the forest just after sunset. Thus the general distribution by day differs from that by night (fig. 1). These vertical movements, which are now known to occur in a number of African mosquitoes and probably also in American species (Nielsen and Nielsen, 1953 ; Snow, 1955) are particularly well shown in the present work on *M. fuscopennata*. Thus when the vertical distribution is considered on an hourly basis (fig. 3) it is seen that, while there is a little activity at the higher levels in the hour after sunrise, activity throughout the rest of the day, as noted above, is virtually confined to ground level. In the hour after sunset, however, there is a sharp burst of activity above the forest, mosquitoes having risen to the 90 and 120-foot levels, which are now the preferred zone, with the 90-foot level slightly in the lead. It is in this hour that males of *M. fuscopennata* swarm regularly over the forest (Part V, p. 292) and at first it was thought that this great surge of activity might be caused by an influx of young females wishing to mate. Corbet (Part VIII, p. 338) has, however, shown that the higher the level the greater the incidence of parous females, an increased percentage being reached in this hour after sunset at 120 feet. In the next hour the pattern of vertical distribution is similar, but biting is now becoming more active once again at ground level, and is decreasing in the zone above the canopy. One hour later ground level has again become the preferred zone and until 05 hours biting above this level (though never quite ceasing) is desultory. In the period

05–06 hours there is another dramatic burst of activity above the canopy, this time lasting for 1 hour only and, further, being confined mainly to the highest (120-foot) zone, where once again the males may be found swarming, but only on warm, clear mornings. Throughout the night the canopy and understorey levels give the impression of a mere zone of passage, all the really intense biting activity being confined to the levels above the canopy in the hours just after sunset and before sunrise, and to ground level during the rest of the night.

TABLE III.—*The biting-cycle of* Mansonia fuscopennata *at Mpanga, by hour and level.* (M_w *has here been multiplied by* 100. T = *No. taken.*)

Hour beginning	Level (feet) 120 (T)	120 (M_w)	90 (T)	90 (M_w)	60 (T)	60 (M_w)	30 (T)	30 (M_w)	G.L. (T)	G.L. (M_w)
12	.	.	.	.	.	.	3	5	107	163
13	.	.	.	.	.	.	5	8	83	132
14	.	.	.	.	2	3	.	.	87	124
15	.	.	.	.	1	2	6	11	100	276
16	.	.	.	.	3	5	7	10	84	139
17	.	.	.	.	3	5	12	15	144	267
18	1342	2470	1596	3269	377	572	155	254	496	1040
19	291	397	531	691	191	266	79	139	325	610
20	60	80	140	144	86	133	56	101	309	517
21	34	33	40	49	45	69	32	47	269	422
22	7	12	24	43	15	27	18	29	284	408
23	3	5	27	31	13	20	15	25	203	270
00	29	16	60	25	20	26	21	27	295	291
01	23	19	67	25	18	23	14	25	225	256
02	12	19	55	19	26	37	24	35	285	259
03	12	15	25	17	18	22	25	37	308	301
04	9	12	37	42	24	24	35	38	309	339
05	423	547	150	199	49	70	66	92	281	408
06	10	6	23	28	10	17	14	23	101	146
07	1	2	.	.	3	5	5	9	74	111
08	.	.	.	.	2	4	2	3	131	171
09	.	.	.	.	.	.	4	6	97	138
10	.	.	.	.	.	.	1	2	67	79
11	.	.	.	.	1	2	2	4	67	97

To complete the picture of biting activity in this mosquito, unpublished work carried out by the writer, mainly in the forest at Zika, near Entebbe, may be quoted. The main part of this work, known as the Entebbe tree survey, consisted of a series of 35 catches, made simultaneously in the canopy, in the understorey and at ground level, five catches each, at seven stations. These catches were carried out over a period of two years. The mean height of the canopy platforms was 57 feet and that of the understorey platforms 35 feet. A very good sample of *M. fuscopennata* was obtained in these catches and the results (Table IV ; fig. 4) are closely comparable with those obtained at corresponding levels in the Mpanga Forest. This type of cycle may, therefore, be taken as showing the type of biting behaviour usual for *M. fuscopennata* in forest in this area.

At Zika, during the work, a local African made a wedge-shaped clearing in the forest edge and established a banana plantation. This was bounded by the forest on two sides, the third abutting on a short-grass area which bounds this part of the Zika forest. The whole plantation was, at its widest, only about 50 yards across,

and it might be thought that the biting-cycle in it should have been much the same as that in the forest. This, however, did not prove to be the case, as five 24-hour catches, carried out in the middle of the plantation, showed a fairly high degree of activity throughout the night, with a rather ill-defined but major wave in the hours preceding midnight (Table IV ; fig. 4*d*). This type of pattern is now associated by the writer with areas through which a given species is passing to some other point, and it is known that at Zika an abrupt departure of *M. fuscopennata* from forest does occur just after sunset (Snow and Corbet, 1959), much after the fashion of some other species of *Mansonia*, and members of some other genera, in America (Snow, 1955).

TABLE IV.—*The biting-cycle of* Mansonia fuscopennata, *by hour and level, in the Entebbe tree survey* (35 *catches*) *and in a plantation and an African hut at Zika* (5 *catches each*). (M_w *has here been multiplied by* 100. T = *No. taken.*)

Hour beginning	Canopy		Understorey		Ground level		Plantation		Hut	
	(T)	(M_w)	(T)	(M_w)	(T)	(M_w)	(T)	(M_w)	(T)	(M_w)
12 .	1	2	9	16	117	175	.	.	.	.
13 .	1	2	2	3	118	180	1	15	.	.
14 .	.	.	5	8	135	226	2	25	.	.
15 .	6	8	4	7	147	265	3	51	.	.
16 .	6	9	5	9	113	189	5	89	.	.
17 .	37	39	16	16	145	268	9	140	.	.
18 .	630	1114	370	655	712	1421	30	435	59	713
19 .	278	476	246	453	453	776	21	304	21	381
20 .	134	215	175	283	397	718	17	329	27	404
21 .	111	187	108	186	344	560	30	561	35	652
22 .	100	175	116	199	353	549	24	368	35	579
23 .	76	127	98	157	275	422	29	534	19	291
00 .	76	138	72	150	288	488	23	427	47	702
01 .	59	105	75	135	310	538	17	323	82	1064
02 .	79	155	91	165	420	683	18	349	84	1407
03 .	115	159	151	189	414	593	27	345	68	1261
04 .	247	234	187	273	405	654	25	306	48	842
05 .	488	744	231	404	466	785	17	272	35	489
06 .	130	207	167	229	235	416	8	136	3	43
07 .	69	64	50	63	147	254	1	15	.	.
08 .	8	11	40	47	124	177	1	15	.	.
09 .	10	16	19	32	190	258	1	15	.	.
10 .	4	5	8	12	129	196	4	64	.	.
11 .	5	5	7	9	103	176	1	15	.	.

A further series of five 24-hour catches was carried out in a hut 80 yards from the forest edge. It is known that the mosquitoes reach this distance 20–25 minutes after sunset (Snow and Corbet, 1959) but the main wave of biting in the hut occurred well after midnight (Table IV ; fig. 4*e*). It is interesting to record that *M. africana* and *M. uniformis* both showed a wave of biting activity in the hut at the same time as *M. fuscopennata* yet observations on these species at Kisumu, Kenya (Haddow, 1942) showed clearly that their principal period of entry was well before midnight. Unfortunately, *M. fuscopennata* was not common at Kisumu, and few were taken entering. Some subsequent evidence, however, suggests that in houses these three species enter at about the same time, early in the night, but do not bite till much later—a pause of this nature is of course known to occur in some other species, as for example in the *Anopheles leucosphyrus* group (Colless, 1956). It is to be noted, however, that these results are not in agreement with the figures recorded by Hadaway (1950) who found a peak of entry before sunset and another before sunrise. Further work is planned to investigate this point.

A good deal of information has now been accumulated about *M. fuscopennata* and, while the present paper is concerned essentially with biting activity, it is felt that an attempt at an integrated picture of its various known circadian activities is worth

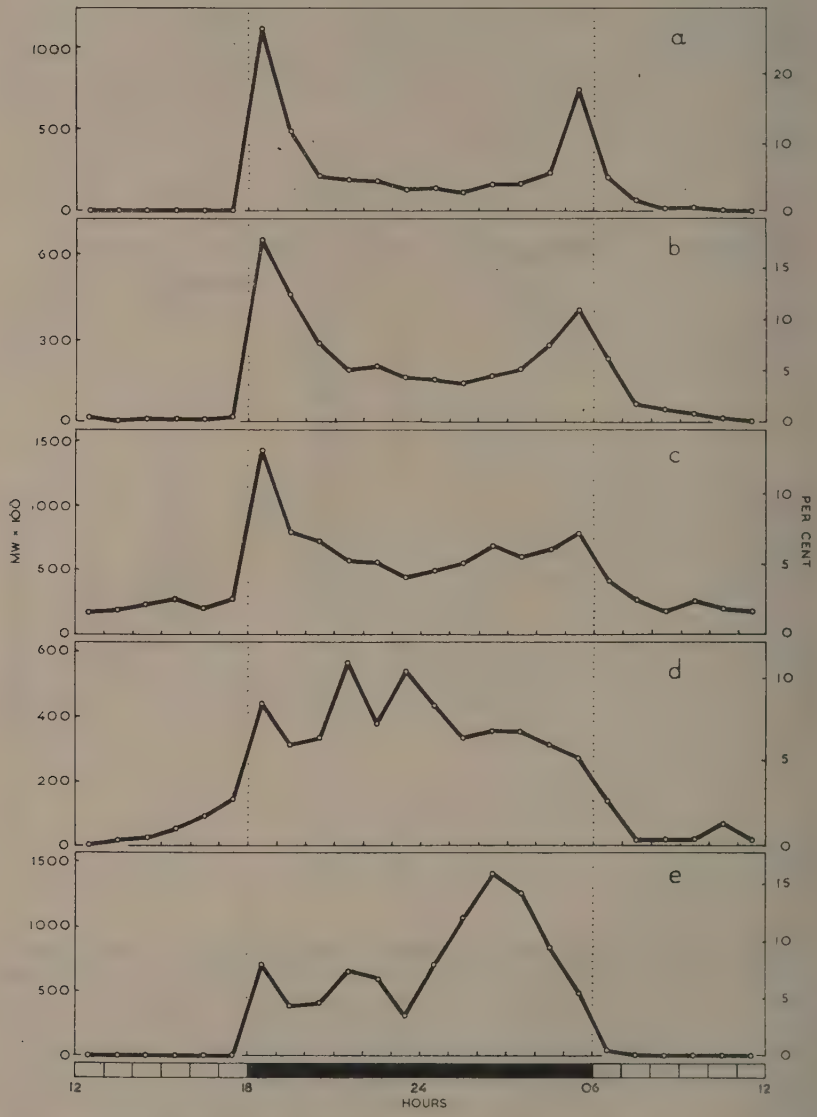


FIG. 4.—The biting-cycle of *M. fuscopennata* at Zika. *a*, forest canopy; *b*, understorey; *c*, ground level (35 catches in each case); *d*, a banana plantation (5 catches); *e*, a hut (5 catches). The scales have been adjusted so that the greatest ordinate is of the same height in each case.

while, even though full interpretation is not yet possible. The information on biting is that given above. That on swarming is taken from Part V, that on oviposition from Haddow and Gillett (1958), that on flight activity from Corbet and Haddow (1961) and Part VI, and that on age-grading from Part VIII. Flight activity

as here referred to means that type which is measurable by the attraction to mercury-vapour light. In figure 5 an attempt has been made to summarise these various activities diagrammatically. In such a diagram, without using very many shades, it is not possible to show the comparison between one strip and another quantitatively. Thus in the diagrams of biting in forest, all levels are shown black for the period 18–19 hours, indicating maximum activity, because activity at all levels did reach its peak for the entire diel at this hour, though it was then much more marked above the canopy than the other levels.

It is unnecessary to recount the changes occurring hour by hour, as this has been done in the case of each of these activities in the papers quoted. The diagram gives, however, some slight idea of the complexity of the circadian patterns of behaviour in this species. Thus the biting pattern varies from level to level in and above the forest, but at all levels in forest the cycle is different from that in plantations, which again differs from that in huts, where entry and biting activity also show entirely different patterns. Flight activity in males goes on all night, whereas swarming is confined to the hour after sunset and to that before sunrise. Male flight activity, however, as shown by trapping at mercury-vapour light, does not show the same pattern inside the forest as outside it. Flight patterns in the female are entirely different from those in the male, and once again that in forest differs markedly from that in the open. The only two activities which show a close parallel are oviposition and the flight of females in forest.

The contention of certain authors that biting activity may be considered as an expression of a general activity rhythm receives no support from the work here discussed. Thus Mattingly (1949*b*) has stated that:

> " The expression ' biting cycle ' as a term in general use, has been employed throughout the present paper. That the phenomena so named represent merely a variation in the urge to bite is, however, very doubtful. The cycle is in fact a record of the frequency with which the mosquitoes come into contact with the bait and, as such, may be accounted for either by the urge to bite or by changes in the general level of activity of the mosquito and, in particular, of its speed and duration of flight ".

This view, most attractive as the time when it was published, no longer covers adequately the known phenomena. We know now, for example, that female *M. fuscopennata* are at the height of their flight activity (as shown by trapping at mercury-vapour light), and so are presumably making contact with the baits freely, at a time when biting is far from active. In the same paper, however, Mattingly introduced (it is believed for the first time in work on the biting Diptera) the concept that intrinsic rhythms might be involved, a view which has since found growing acceptance and which calls for much more study than it has since received.

It has further become obvious that no single explanation can be applied to all the varied cyclic activities here discussed. Recently Corbet (1960*b*) has emphasised that in dealing with insects in nature it is necessary to appraise the interplay between environmental influence (obviously very strong in *M. fuscopennata*) and persistent endogenous rhythms. In the present case it is obvious that if endogenous rhythm is involved there must be more than one such rhythm. There is, of course, no obstacle to the view that multiple persistent rhythms may occur, if the attractive theory of Harker (1958) be accepted. Her suggestion is that all cells have a basic 24-hour rhythm, but that the rhythm in one group of cells is not necessarily in phase with that in others. Thus there may be multiple " clocks ", each of which may have been " set " at a different phase of the diel. Even Harker's theory, however, does not explain the differences in the timing of a single activity (biting, for example) in different environments. Here we must postulate a strong environmental influence and, indeed, it is clear that crepuscular light is very important in some of the activities discussed. As Corbet (1960*b*) has pointed out, an activity continuous through-

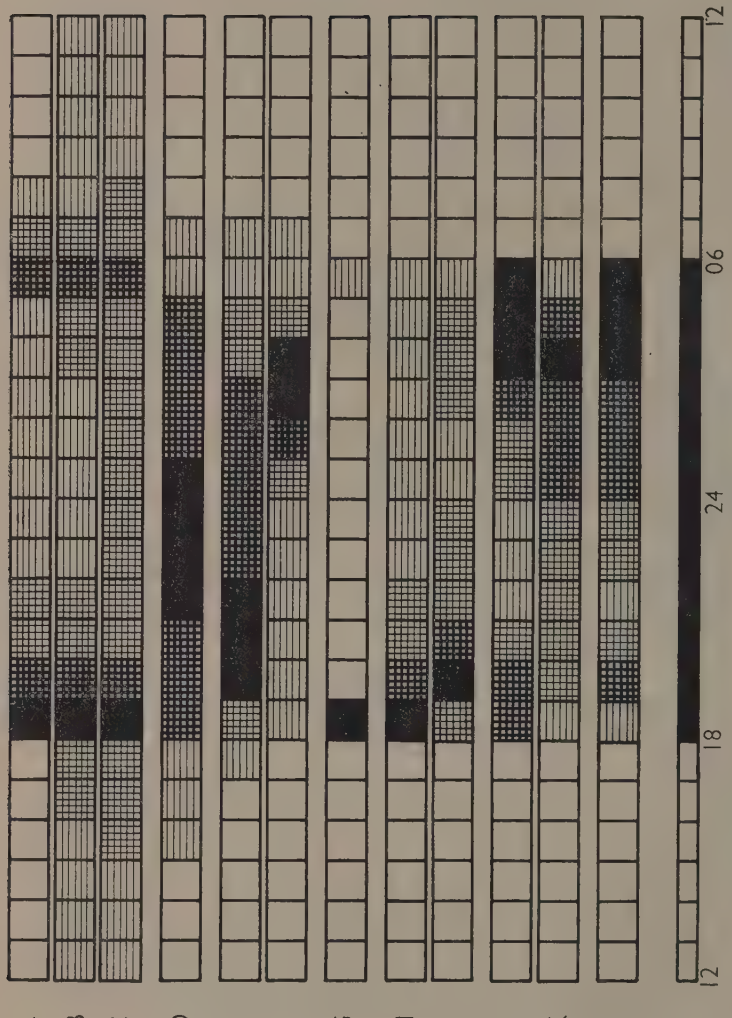


FIG. 5.—Synoptic figure of the circadian rhythms shown by *M. fuscopennata* in the Entebbe area. Five grades of activity are shown, from zero (white) to maximal activity (black). For further explanation see text. A, Biting activity above the canopy; B, biting activity in the canopy and understorey; C, biting activity at ground level in forest; D, biting activity in a banana plantation; E, probable entry to huts; F, biting activity in huts: G, swarming activity; H, attraction of males to mercury-vapour light in forest; I, the same, in the open, some distance from forest; J, attraction of females to mercury-vapour light in forest; K, the same, in the open, some distance from forest; L, oviposition.

out the entire diel cycle may, none the less, be greatly stimulated in one or both of the crepuscular periods, as in *Ae. cumminsii* (quoting here the results of Haddow, 1960) and *M. fuscopennata* (quoting the present work).

In concluding this account it is necessary to emphasize that in *M. fuscopennata* there are probably other activities involving a 24-hour rhythm. Mating is probably cyclic and, at most, only a small fraction of it can occur in the male swarms (Part V, p. 297). It may be that pupation and emergence also show a circadian pattern, as this is known to be true of certain mosquitoes, such as *Ae. taeniorhynchus* (Nielsen and Haeger, 1954), though others, such as *Ae. aegypti*, show no sign of such a rhythm (Haddow, Gillett and Corbet, 1959). Broadly speaking, therefore, an immense amount of work remains to be done.

M. aurites and *M. fraseri*

Previous work in Bwamba and at Zika has shown that *M. aurites* is essentially arboreal in its biting habits (though it may rest in fair numbers in low undergrowth by day) and studies by Williams, Weitz and McClelland (1958) and by McClelland and Weitz (1960) have shown that both *M. aurites* and *M. fraseri* feed almost exclusively on birds.

Up till the present the largest catches of both species had always been made in the canopy, but the work here discussed revealed that they appear to be commoner still in the air above it. Though the numbers taken were small, the distribution was clearly marked, the combined results for the two species being :

Level	No. taken
Above the canopy	35
Canopy and understorey	7
Ground level	0

As in previous work, both species were found to be markedly crepuscular, and of the 42 specimens taken 25 (60 per cent.) were obtained in the single hour after sunset. The cycle, in the case of *M. aurites*, is shown in Table II and figure 9.

Here we have one of those cases where there is a very great deal of apparent ecological " overlap " between two sympatric species. They are very similar in appearance, both being richly golden mosquitoes with fairly restricted black markings ; both this and previous studies suggest that they bite at the same time and at the same level, and the preferred host is the same in both cases. It has been shown however, that there are very pronounced differences in the form of the egg-rafts (Gillett, 1961) and also in the morphology of the larvae and pupae (Gillett, 1946). Available evidence thus suggests that the avoidance of overlap may depend, in this case, on differences in the ecology or habitat of the immature stages.

It might be concluded, from the vertical distribution, that these mosquitoes were approaching the forest from outside and " profiling " over it before settling. Work in the Entebbe area has, however, shown that males of both species, together with fed and unfed females, rest at ground level in forest in very large numbers by day (they are much more abundant in forest than in any other environment) and on occasion they may be watched actually rising through it at dusk (Haddow, 1954). In other papers in this series (Parts II, p. 257 and XII, p. 360) it has been shown that where microclimate is concerned, the upper canopy level presents a simple edge effect, such as that described by Haddow (1945*a*) as existing between the forest edge and the open air at ground level. The differences which do exist by day, and which may well form a microclimatic barrier for some species thus tend to break down at sunset or even before, in some areas (as noted by Boshell and Osorno, 1944), and there is no longer any effective climatic barrier to deter mosquitoes from diffusing outward from the forest edges, or upward through the canopy into the open air above. It is believed that the two species under discussion do so, and it is to be

noted that the males also are known to be active above the forest, swarming there in the hour after sunset (Part V, p. 290).

M. africana and *M. uniformis*

Unfortunately, both these interesting mosquitoes were scarce at Mpanga. It is interesting, however, to note that of 20 taken in all, 13 were obtained above the canopy. The arboreal tendencies of *M. africana* have already been commented on, as in catches carried out simultaneously at different levels in the Semliki Forest 35 per cent. of the total were taken at heights over 50 feet (Haddow, Gillett and Highton, 1947). Both *M. africana* and *M. uniformis* will attack many kinds of host (Williams, Weitz and McClelland, 1958) and they have been recorded by the writer as occurring freely in the canopy in numerous lowland forests in Uganda.

TABLE V.—*The biting-cycle of* Aedes apicoargenteus *at Mpanga, by hour and level.* (*M_w has here been multiplied by* 1000. *T = No. taken*)

Hour beginning	Level (feet) 120 (T)	120 (Mw)	90 (T)	90 (Mw)	60 (T)	60 (Mw)	30 (T)	30 (Mw)	G.L. (T)	G.L. (Mw)
00	.	.	.	.	.	.	.	.	.	.
01	.	.	.	.	.	.	.	.	.	.
02	.	.	.	.	.	.	.	.	.	.
03	.	.	.	.	.	.	.	.	.	.
04	.	.	.	.	.	.	.	.	.	.
05	.	.	1	17	.	.	.	.	.	.
06	1	17	3	46	.	.	.	.	.	.
07	1	17	3	53	1	17	2	35	1	17
08	.	.	2	35	23	360	11	180	1	17
09	1	17	6	94	23	384	24	351	4	64
10	1	17	2	35	30	392	36	455	14	247
11	1	17	3	57	34	488	39	648	15	205
12	1	17	8	132	48	528	75	1077	33	565
13	.	.	3	53	55	713	63	762	29	524
14	.	.	7	113	51	428	81	960	14	205
15	1	17	6	102	54	676	76	1104	24	314
16	.	.	6	102	49	487	60	910	6	109
17	.	.	16	239	14	243	23	331	3	46
18	2	35	2	28	3	53	5	46	.	.
19	.	.	.	.	.	.	.	.	.	.
20	.	.	.	.	.	.	.	.	.	.
21	.	.	.	.	.	.	.	.	.	.
22	.	.	.	.	.	.	.	.	.	.
23	.	.	.	.	.	.	.	.	.	.

Aedes longipalpis

The sample was very small, but as usual this mosquito was diurnal (Table II) and occurred mainly in the canopy (Haddow, Gillett and Highton, 1947). The vertical distribution is shown in Table I and figure 1.

Ae. ingrami

In all work round Entebbe, *Ae. ingrami* has been found to be a mosquito which bites mainly in the understorey, though it is known to make cyclic vertical movements (Haddow, 1954). At Mpanga, this preference for the understorey was confirmed (Table I ; fig. 1). This species showed, as in other work carried out in the area, a peak of biting activity in the hour before sunset (Table II ; fig. 9).

Ae. apicoargenteus

This was the most abundant member of the genus *Aedes* at Mpanga and, in order to discuss it adequately, it will be necessary to include other work carried out in the Entebbe area and very extensive series of catches made in the Semliki Forest in Bwamba County, in western Uganda.

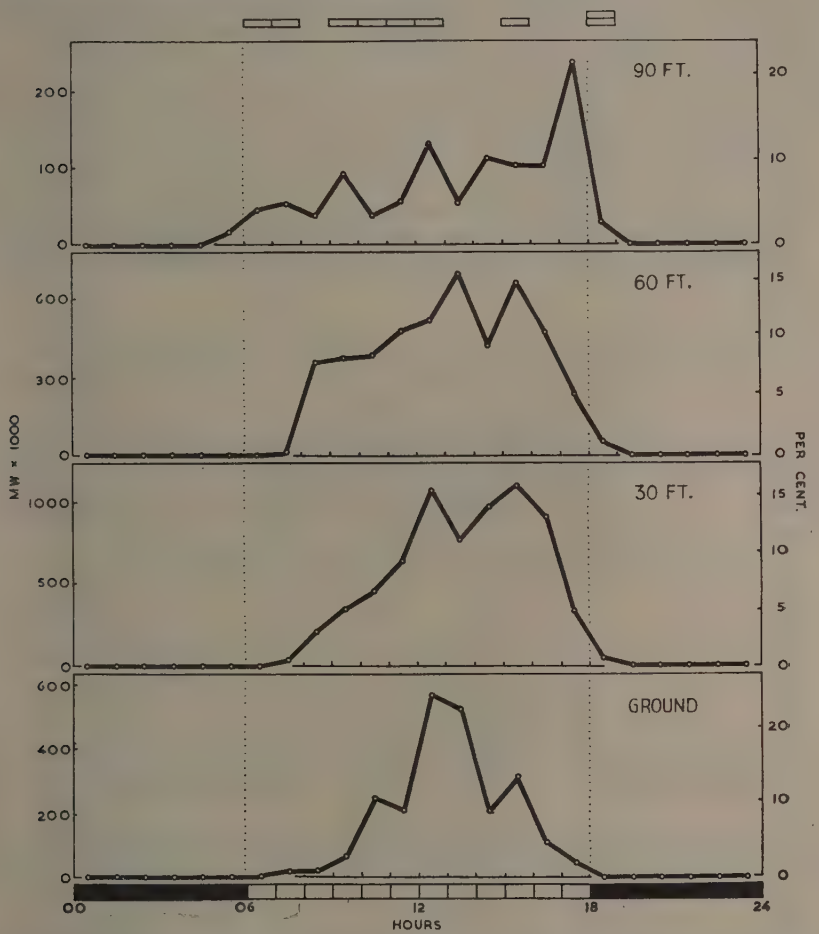


FIG. 6.—The biting-cycle of *Ae. apicoargenteus* at Mpanga by hour and level. The graphs show the results for 90 feet, 60 feet, 30 feet and ground level. The numbers taken at 120 feet were too small to permit construction of a graph. They are shown by blocks above the top figure. The scales have been adjusted so that the greatest ordinate is of the same height in each case.

Ae. apicoargenteus is essentially an understorey mosquito, though it is also fairly prevalent in the canopy. During the Mpanga catches it was commonest in the canopy when the weather was cool and overcast. The vertical distribution is shown in Table I and figure 1.

The biting-cycle at Mpanga was somewhat irregular but markedly diurnal (Table V ; fig. 6). At ground level there was a well-marked but fairly brief peak of activity just after midday. At 30 and 60 feet the wave began at about the same time, but was continued for much longer. At 90 feet the peak did not occur till late afternoon

(presumably when the wind was dropping). Unfortunately numbers at 120 feet are inadequate for the production of a graph, but it is interesting to note that of the nine specimens taken biting at this level two occurred in the hour after sunset; in the total of 1101 *Ae. apicoargenteus* taken at Mpanga, only 12 were taken by night (all in this hour). The first picture is thus of a diurnal mosquito presenting a rather irregular biting-cycle whose peak of activity occurs in the afternoon, tending to become later and later with increasing height above ground.

TABLE VI.—*The biting-cycle of* Aedes apicoargenteus *by hour and level in the Entebbe tree survey and in the various series of catches made in Bwamba County. The Bwamba canopy sample comprises the Mongiro-Mamirimiri catches and the Bwamba tree survey. The understorey sample comes entirely from the Mongiro-Mamirimiri catches as these were the only understorey catches made in Bwamba. The ground level sample comprises the first forest catches, the Mongiro-Mamirimiri catches and the Bwamba tree survey.* (M_w *has here been multiplied by* 1000. T = *Number taken*)

Series	Entebbe tree survey						All Bwamba catches combined					
Level	Canopy		Understorey		Ground		Canopy		Understorey		Ground	
Number of catches	35		35		35		300		80		295	
Hour beginning	(T)	(M_w)	(T)	(M_w)	(T)	(M_w)	(T)	(M_w)	(T)	(M_w)	(T)	(M_w)
00	1	20	.	.	.	.	.	.	.	.	.	.
01	1	20	.	.	.	.	1	2	.	.	.	.
02	.	.	1	20	.	.	.	.	.	.	.	.
03	.	.	.	.	.	.	.	.	.	.	.	.
04	.	.	.	.	.	.	.	.	.	.	.	.
05	1	20	.	.	.	.	.	.	.	.	.	.
06	5	79	3	61	1	20	4	9	4	35	.	.
07	17	247	23	365	15	207	7	16	4	35	4	9
08	14	238	20	268	16	257	30	65	9	74	1	2
09	39	437	44	650	40	429	23	52	3	27	1	2
10	38	560	46	697	49	549	29	62	13	114	6	14
11	21	349	26	473	24	315	26	59	6	53	3	7
12	15	255	18	327	12	190	34	78	21	140	6	14
13	14	255	12	181	10	169	43	117	19	146	6	12
14	15	282	18	360	3	61	56	127	24	190	5	12
15	16	258	19	358	4	82	72	155	19	126	8	19
16	16	306	15	238	7	140	50	114	15	117	7	16
17	15	271	21	404	5	95	37	80	4	35	3	7
18	4	82	5	104	1	20	10	20	.	.	1	2
19	.	.	1	20	.	.	4	9	.	.	.	.
20	1	20	1	20	.	.	1	2	.	.	.	.
21	.	.	.	.	.	.	1	2	.	.	.	.
22	.	.	1	20	.	.	.	.	.	.	.	.
23	.	.	.	.	.	.	.	.	.	.	1	2

The matter is not, however, so simple, as in other areas *Ae. apicoargenteus*, while always diurnal, may show quite different patterns of biting activity. Thus in the Entebbe tree survey, which has been described above, the peak occurred at the same time at ground level, in the understorey and in the canopy, and it occurred before, not after midday (Table VI; fig. 7). During work in Bwamba County, very large numbers of catches were made in the Semliki Forest, as follows:

(1) A series of 15 catches at ground level (Haddow, 1945*a*).

(2) A series of 40 catches made simultaneously at different levels. The details were : In the first locality, Mongiro, there were 20 catches, the levels being ground, low understorey, high understorey and canopy. In the second locality, Mamirimiri, there were also 20 catches, the levels being ground, low understorey, high understorey, mid-canopy and high canopy (Haddow, Gillett and Highton, 1947).

(3) The Bwamba tree survey. This comprised 240 catches, made simultaneously at ground level and in the canopy, six each at 40 different forest stations.

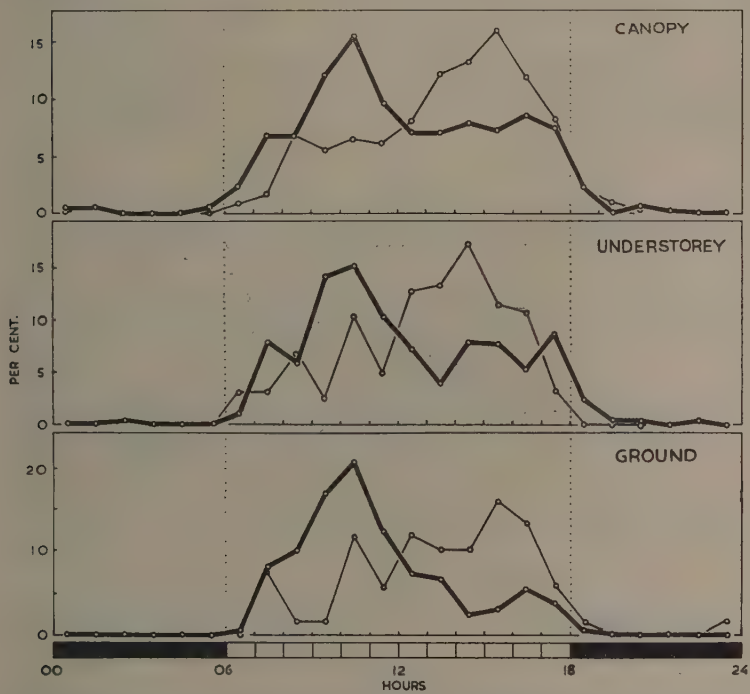


FIG. 7.—The biting-cycle of *Ae. apicoargenteus* by hour and level in Zika forest (thick line) and in Bwamba (thin line), in canopy, understorey and at ground level. The scales have been adjusted so that the greatest ordinate is of the same height in each case.

There are thus 295 catches in all at ground level, 80 in the understorey and 300 in the canopy, carried out over a period of years. As throughout this work the trend remained very similar, it is thought permissible to combine all these series as otherwise, *Ae. apicoargenteus* being less common in the Semliki Forest than in the Entebbe area, the ground-level sample would be too small for discussion (Table VI ; fig. 7).

Here once again the cycle at all levels is very similar, but it differs entirely from that observed at Zika in that the peak occurs well after midday, rather as in the understorey and canopy at Mpanga. It might be concluded that the late biting peak seen at Mpanga and in Bwamba is characteristic of heavy rain forest, and that the early biting peak, as seen at Zika, might be characteristic of the lighter, less mature and more " cut over " type of forest which is found there. Equally, it could be maintained that at Zika afternoon biting is curtailed by the regular lake breeze, and that activity would have continued to build up until afternoon had this factor not proved dominant.

A further complication appears, however, when the results of a long series of 24-hour catches, carried out in the canopy at Zika No. IV station, are considered. Altogether 821 *Ae. apicoargenteus* were obtained in this series, which comprised sixty catches, carried out at weekly intervals. The results (fig. 8) have been analysed in a number of different ways, the clearest picture being given when groups of twenty

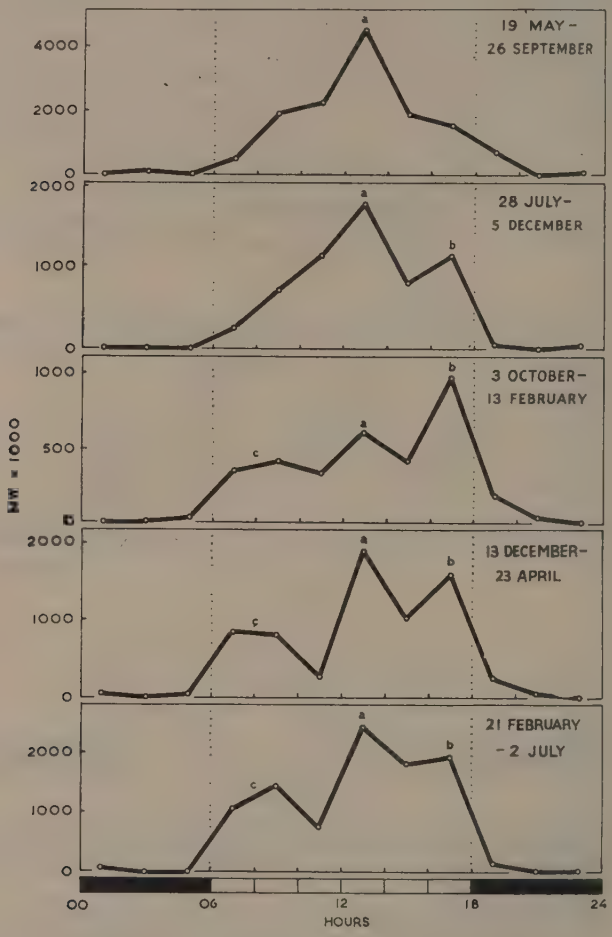


FIG. 8.—The biting-cycle of *Ae. apicoargenteus* in 60 catches on No. IV canopy platform at Zika. The catches are arranged in groups of 20 with a 50 per cent. overlap: 19th May to 26th September; 28th July to 5th December; 3rd October to 13th February; 13th December to 23rd April; 21st February to 2nd July. The 1st, 3rd and 5th graphs thus have no overlap, and between them cover the whole series. The scales have been adjusted so that the greatest ordinate is of the same height in each case. (For explanation of *a*, *b* and *c*, *see* text, p. 333.)

catches are used on a 2-hour basis. This rather coarse grouping has been employed as, though some of the samples are large, others, from the drier periods of the year, are rather small for a 1-hour grouping. The successive groups have a 50 per cent. overlap, being catches No. 1–20, 11–30, 21–40, 31–50 and 41–60. Thus the top, middle and bottom graphs in figure 8 are mutually exclusive, covering catches 1–20, 21–40 and 41–60.

It is here seen that in the first group of catches there is a clearly marked single peak, just after midday, which has been labelled *a*. In the second group this peak is still apparent, but another—*b*—has begun to appear in the later afternoon. In the third group of catches *b* has become the dominant peak, *a* being much reduced. In the fourth group the trend has been reversed, and *a* is once again rising while

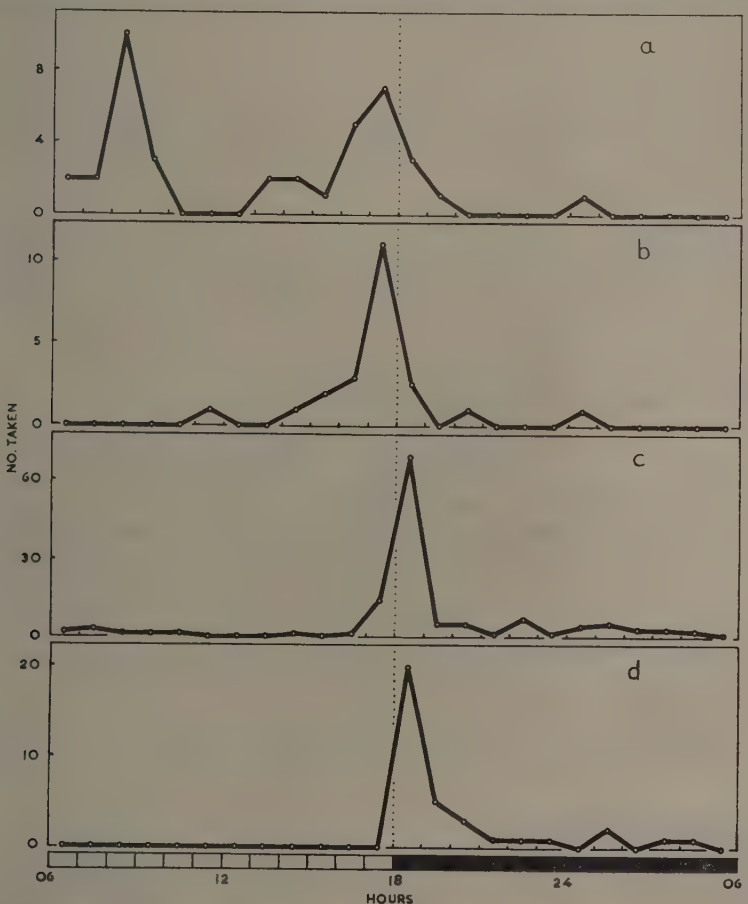


Fig. 9.—The biting-cycles of four of the less abundant species, regardless of level. As the numbers are small in three cases, arithmetic totals have here been used. The scales have been adjusted so that the greatest ordinate is of the same height in each case. *a*, the *Ae. tarsalis* group; *b*, *Ae. ingrami*; *c*, *C. annulioris*; *d*, *M. aurites*. In the case of *C. annulioris* the hourly M_W has also been worked out and is given in Table II.

b decreases. In the last group *a* is once more the dominant peak. There is perhaps a separate wave in the last three groups—*c*—but this is not sufficiently distinct to be worthy of comment.

It is unfortunate that this apparent oscillation of the biting peak was not noted till after the field work had been completed. Had it been recognised, during the catches, that a distinct trend was appearing, an extra twenty or so would have been carried out to cover once more the period shown in the first group, in order to determine whether, at the same time of year, peak *a* regained its clearly dominant position. The trend in the last two groups certainly seems to be in this direction.

These results are not, of course, conclusive, but they are highly suggestive of an external influence moulding a biting pattern which is at any time (apart from its general diurnal nature) poorly defined. There is some reason to believe that *Ae. apicoargenteus*, though a sylvan species, prefers the lighter parts of the forest. Thus Garnham, Harper and Highton (1946), working in the Kaimosi Forest in Kenya, found it most prevalent in secondary forest with broken canopy; Laarman (1958) noted that it bred most freely in high tree-holes and would oviposit in forest clearings; Surtees (1959) also found a preference for breeding at the higher, lighter levels, and Corbet (Part IV, p. 278) found that at Mpanga the highest incidence of oviposition in bamboo containers on the tower was actually at the levels above the canopy. These observations, taken together with the facts that both biting and oviposition (Haddow, Corbet and Gillett, 1960) are diurnal, suggest that light has a very important influence on *Ae. apicoargenteus*. Such being the case, the alterations in time of maximum biting activity as seen in the Zika No. IV series might easily be due to seasonal changes in the density of the foliage, or to seasonal differences in the angle of the sun. Further observation is clearly called for, and an investigation of this point at Zika is planned. That seasonal changes in biting behaviour might occur in other mosquitoes (*e.g.* in *A. gambiae* (Haddow, 1954)) was already known, but those here discussed are of a much more pronounced order. *Ae. apicoargenteus* poses, at the moment, some of the more baffling questions concerning the mechanisms underlying cyclic biting behaviour.

Ae. africanus

Little can be said of this important mosquito. The known biting-cycle shows a clear peak of activity in the hour after sunset (Haddow, Gillett and Highton, 1947) and the fact that in the present series equal numbers bit in the hour before and that after sunset (Table II) may be discounted on account of the small size of the sample. It is interesting to note that of the 16 specimens obtained exactly half came from levels above the canopy.

Ae. tarsalis group

As usual these mosquitoes were ground-haunting and showed (fig. 9) the biphasic peak characteristic of this group (Haddow, 1960).

Eretmapodites semisimplicipes

In the writer's past experience members of this genus are rarely taken much above ground level (Haddow, 1956*b*), so it is interesting to find that five of the six specimens taken were obtained in the canopy and understorey (Table I). Other work at Mpanga has, however, shown that in at least one other activity this species ranges freely into the upper levels, larvae being found in bamboo containers in substantial numbers up to canopy level, and in smaller numbers up to 90 feet, above the canopy (Part IV, p. 280).

Culex annulioris

This species characteristically occurs at all levels in forest, but is always much more abundant at ground level than at any other. At Mpanga its vertical distribution (Table I; fig. 1) was thus typical, and it showed a sharp peak of activity in the hour after sunset (Table II; fig. 9), as in the writer's other series in the Entebbe area (*unpublished*). It is to be remembered, however, that Williams (1956), using fowls as bait, found that in one locality there were two peaks of activity, one in the late afternoon and the other in the early night.

Haematopota ugandae

All six specimens obtained were taken at ground level (Table I) and by day, five of them in mid-morning. It would be wrong, however, to class this as an exclusively ground-haunting and diurnal species. Thus Corbet (Part V, p. 309) has taken both males and females by night at mercury-vapour light-traps on the tower. In his catches females occurred at 30 feet as well as at ground level, but the males all occurred at 120 feet.

Chrysops centurionis

This species was scarce at Mpanga, but showed its usual arboreal and crepuscular habits (Haddow, Gillett, Mahaffy and Highton, 1950).

Acknowledgments

The writer wishes to thank Dr. Philip S. Corbet for taking over identification and supervision at times when he was unavoidably absent, and Messrs. Yovani Senkubuge and Christopher Mawejji for their excellent work in the field.

Summary

1. A series of forty 24-hour catches was carried out on the steel tower in Mpanga Forest. The catches, made simultaneously at ground level and at 30, 60, 90 and 120 feet, were made at weekly intervals, with human bait.

2. Numerous species of mosquitoes, and two tabanids, were taken, but few were abundant. The biting-cycles and vertical distribution of the less common species are discussed briefly and compared with results obtained elsewhere.

3. Two species, *Mansonia fuscopennata* and *Aedes apicoargenteus*, were very common.

4. To permit full discussion of *M. fuscopennata*, the results of other series of catches in forest, a banana plantation and a hut in the Entebbe area are described. It is shown that the biting-cycle of this mosquito varies from level to level and from one environment to another, and that it makes daily vertical migrations. Further, a synthesis of what is known of circadian rhythm in this species is attempted. It is shown that the swarming, flight activity and oviposition-cycles all differ from any of the biting-cycles described and that there are sexual differences, as well as environmental differences, in some of the patterns of activity.

5. In *Ae. apicoargenteus* the results are confined to forest, but here again the results of other series of catches in the Entebbe area and of very extensive series made in the Semliki Forest are included to permit wider discussion of biting behaviour, which is always diurnal. At Mpanga the biting-cycle showed differences from level to level, but in previous work at Entebbe and in the Semliki Forest it has shown much the same pattern at all levels. The timing of the main wave of activity varies from place to place, however, and in one series there was evidence of seasonal change in the cycle. It is considered that there is a strong environmental influence in action, and that this is probably light.

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA.

VIII. THE AGE-COMPOSITION OF BITING MOSQUITO POPULATIONS ACCORDING TO TIME AND LEVEL

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Introduction

Mattingly (1949*a*) suggested that in *Mansonia africana* there might exist two sections of the population, each with a different behaviour, and that the relative proportions of these sections in the whole population would determine the form of the biting-cycle for that species. Shortly after this, Downes (1950) pointed out that the sections of mosquito populations showing different behaviour might represent age-groups, and Lumsden (1952) developed these ideas to advance the hypothesis that the two components of the population were nulliparous and parous females, respectively. This suggestion has implications of the greatest importance where field studies of biting insects are concerned (*see* Haddow, 1954): from an epidemiological point of view it is clearly desirable to know whether older (and therefore potentially infective) individuals bite more often at certain times, and when activity cycles are being interpreted it is also important to know the extent to which these may have been influenced by the age-composition of the population at the time when the observations were made.

Earlier investigations of this question have been limited in scope by the methods available for age-determination, and it is only recently that techniques have developed whereby the physiological age of individual female mosquitoes can be unequivocally recognised (*see* Detinova, 1959). Studies undertaken so far, however, have revealed no clear-cut differences in cyclical activity between young and old adult mosquitoes. Senior White (1953), using the ovarian stages of Christophers (1911) to distinguish the younger nulliparous females of *Anopheles aquasalis*, observed that fewer of them came to bite in the second hour after sunset than in the two preceding hours, but this difference was not large. Gillett (1957), using the presence of hydrachnid mites to recognise young females of *M. africana*, detected no significant variation in the proportions of parasitised females biting throughout the night; and Haddow and Gillett (1958) found that females of *Mansonia fuscopennata* which contained relict eggs, and which were therefore known to be parous, formed a steady percentage of those biting between sunset and sunrise. Gillies (1957) made a detailed study of *Anopheles gambiae*, in which females biting throughout the night were assigned to one of three age-categories. The first contained pre-gravids (Gillies, 1954) biting for the first time; the second contained gravids, and the third, gravids which were infected with sporozoites and which were therefore at least 13 days old. In addition, Gillies recorded the fertilisation index of the pre-gravids. From his examination of 3296 females, Gillies concluded that, although younger females were slightly more active before 2200 hours, their pattern of feeding did not differ materially from that of older females, and the gross features of the biting-cycle were therefore not being determined by age-groups behaving as distinct populations.

Studies on other families of Diptera, however, have revealed significant differences in the ages of females biting at different times. Lewis (1953) found that, at Mvolo in the Sudan, the proportion of *Simulium damnosum* infected with *Onchocerca* worms, and therefore parous, was higher in flies biting before 1 p.m. than in those caught later in the day. Subsequently, by using three independent age-criteria, this author showed

that significantly more parous females of *S. damnosum* bit in the morning also in the Tonkolili Valley, Sierra Leone (Lewis, 1956*a*). In Northern Nigeria, however, both Crosskey (1958) and Lewis (1958) found that more old flies bit shortly before and after midday, the younger flies biting more in the early morning and late afternoon. In Britain, older females of *Simulium ornatum* were found by Davies (1957) to bite mainly in the hour before dusk, a phenomenon which he attributed to the less severe environmental conditions prevailing at that time. Finally, the work of Duke (1959) on Tabanidae in the Southern Cameroons should be mentioned. From the dissection of over 10,000 specimens of *Chrysops silacea* and *Chrysops dimidiata* (Bombe form), Duke observed that in both species the proportion of females infected with *Loa* parasites was greater in the afternoon than in the morning, but that this difference was significant only in the case of *C. silacea.*

Although these studies have revealed consistent differences in the age-composition of biting populations according to the time of day, it must be stressed that these differences have seldom been large enough to affect the gross pattern of the biting-cycles of the species concerned. That is to say, conclusions based on the general form of the biting-cycle would in most instances be the same whether the biting population had been mainly nulliparous or mainly parous.

To investigate this question further, a study was made of the ages of mosquitoes coming to bite at different times and levels on a tower in Mpanga Forest, Uganda (Part I). Only one species, *M. fuscopennata*, was sufficiently abundant to be studied in detail, but this was appropriate for the purpose, since the biting-cycle in forest (Haddow, 1956*a*) is biphasic and thus any effects caused by the differential activity of age-groups should be clearly discernible. Studies on other species were limited by the material available.

Methods

The mosquitoes were obtained by Haddow in 24-hour catches with human bait at Mpanga (Part VII, p. 315), and were passed to me after having been identified and sorted according to hour and level. Each catch began at 12 hours " catch-time ", sunset being designated as 18 hours (Lumsden, 1952). Mosquitoes were examined from 13 catches, which were made between 14th October, 1958 and 12th May, 1959. The usual procedure for handling material was as follows: mosquitoes caught between 12 and about 06 hours remained alive until about 09 hours when they were killed by refrigeration at *ca.* —25° C. Those caught subsequently (06–12 hours) were usually killed before 17 hours the same evening. Mosquitoes were then stored at —25° C. until it was convenient to examine them. Under such conditions they remained fresh for at least two months, though seldom for as long as five. They were dissected in batches of about 75, and classified as either nulliparous or parous by a rapid combined technique (Corbet, 1959*a*), which makes use principally of the condition of the ovarian tracheoles (Christophers, 1911 ; Detinova, 1945), and secondarily, in doubtful cases, of the presence of follicular relics (Colless, 1958). Adoption of tracheolar coiling as the primary criterion was particularly useful when classifying *M. fuscopennata*, a species in which the follicular relics are seldom visibly pigmented.

The measure of central tendency used in the analysis of results is Williams' mean (M_w) (*see* Part I, p. 253), sometimes expressed here as a percentage (*see* Haddow, 1960). The age of samples is expressed as the nulliparous rate, which is the percentage of females that are nulliparous. This is a more suitable index to adopt than the percentage which are parous. The nulliparous fraction is relatively homogeneous, in that its members have never laid eggs, whereas the parous fraction will probably contain females which have oviposited once, and others which have done so more frequently.

TABLE I.—*Incidence of nulliparous (N) and parous (P) females of* Mansonia fuscopennata *in* 13 *baited catches at Mpanga, grouped according to hour and level.* (100 M_w—*Williams' mean* × 100.)

Hour beginning (catch-time)	Height in feet: Ground level N Total	Ground level N 100 M_w	Ground level P Total	Ground level P 100 M_w	30 N Total	30 N 100 M_w	30 P Total	30 P 100 M_w	60 N Total	60 N 100 M_w	60 P Total	60 P 100 M_w	90 N Total	90 N 100 M_w	90 P Total	90 P 100 M_w	120 N Total	120 N 100 M_w	120 P Total	120 P 100 M_w	All levels N Total	All levels N 100 M_w	All levels P Total	All levels P 100 M_w
12	26	140	20	113	2	11	1	5	.	.	.	.	.	.	.	.	.	.	.	.	28	156	21	120
13	31	158	20	120	1	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	32	161	20	120
14	31	138	14	69	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	31	138	14	69
15	27	146	17	99	1	5	1	5	1	5	.	.	.	.	.	.	.	.	.	.	29	164	18	89
16	17	85	8	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17	85	8	50
17	26	157	27	144	6	16	.	.	.	.	1	5	.	.	.	.	.	.	.	.	32	187	28	149
18	141	700	63	377	39	219	26	102	99	542	53	185	451	2664	223	1395	278	1735	190	1157	1008	6379	555	3517
19	93	520	36	220	27	175	12	72	52	247	28	118	116	645	82	455	67	294	61	277	355	2182	219	1293
20	90	450	20	89	16	86	9	51	22	115	18	101	34	153	21	106	21	101	16	70	183	1056	84	459
21	68	336	24	107	11	54	7	42	10	55	5	28	16	86	20	112	13	48	16	58	118	616	72	398
22	84	415	39	154	4	21	3	17	2	11	5	28	8	45	4	24	3	15	.	.	101	541	51	253
23	55	228	21	101	4	24	2	11	4	17	2	11	5	28	1	5	1	5	2	9	69	307	28	168
00	73	187	16	76	4	24	1	5	4	21	.	.	4	17	3	15	1	5	2	11	86	253	22	108
01	55	170	10	46	5	24	.	.	2	11	3	15	3	15	.	.	5	24	2	11	70	326	15	65
02	68	250	22	113	8	44	3	17	3	15	3	15	.	.	.	.	3	17	1	5	82	359	29	171
03	87	351	53	251	4	21	5	24	1	5	2	11	5	25	1	5	2	11	3	15	99	416	64	307
04	81	270	28	136	6	35	2	11	1	5	1	5	8	44	6	23	1	5	1	5	97	390	38	198
05	93	459	27	126	17	88	8	37	13	67	8	44	19	97	27	113	104	494	102	478	246	1345	172	843
06	29	132	16	70	1	5	4	21	1	5	3	17	5	24	5	19	.	.	.	.	36	179	28	126
07	13	66	13	62	1	5	.	.	.	.	2	9	.	.	.	.	.	.	.	.	14	70	15	70
08	29	139	22	104	.	.	2	9	.	.	1	5	.	.	.	.	.	.	.	.	29	136	25	134
09	35	153	12	67	1	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	36	156	12	67
10	25	107	13	58	1	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	26	108	13	58
11	21	117	5	28	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	21	117	5	28
Totals	1298	.	546	.	159	.	86	.	215	.	135	.	674	.	393	.	499	.	396	.	2845	.	1556	.

In the following account, an observation is sometimes expressed thus: " Females at *A* are younger than those at *B*", when what is implied is that " the nulliparous rate of samples of females biting at *A* is higher than that of those biting at *B* ". This slightly incorrect phraseology is adopted in the interests of brevity. Nulliparous females are referred to as " nullipars " and parous females as " pars ".

The detailed records on which this study is based will be deposited in the archives of the British Museum (Natural History), London.

Results

Mansonia fuscopennata

Combined results for the 13 catches appear in Table I, in which nullipars and pars are recorded separately and grouped according to hour and level.

These data reflect the biting-cycle of *M. fuscopennata* at Mpanga (Part VII, p. 319). During the day, biting activity is virtually restricted to ground level, whereas at night it occurs at all the levels sampled, reaching peaks of intensity in the hour after sunset, and in the hour before sunrise. These two peaks, which give the biting-cycle its characteristic form, become progressively better defined at higher levels. Thus at ground level substantial biting occurs throughout the night, but at 120 feet it is largely confined to the two peak periods.

Table II.—*Percentage nulliparous in total catches of females of* Mansonia fuscopennata *at different levels*

Level and time	Percentage nulliparous based on Arithmetic mean	Williams' mean
Night (18–06)		
120 . .	55·7	54·0
90 . .	63·3	61·5
60 . .	62·5	60·9
30 . .	65·0	66·6
Ground . .	73·4	72·2
Day (06–18)		
Ground . .	62·4	60·2

This temporal and spatial distribution of biting activity must be allowed for when the age-composition of females at different levels is being measured. Thus in Table II inter-level comparisons only involve those females biting at night.

The values in Table II fall in the same sequence whether the nulliparous rates are calculated as arithmetic means or as Williams' means. Some of the differences recorded between levels are highly significant, and furthermore show consistency from one catch to another (Table III). For example, in 13 observations, the females biting at night at 120 feet were older than those at 90 feet on 10 occasions, and those at 90 feet were older than those at ground level on 11. These three levels were the only ones at which catches were consistently large, and therefore the highly significant differences which exist between them must be regarded as strong evidence that the average age of biting females increases progressively from ground level to 120 feet. The positions of other level-groups in this sequence are consistent with this trend. The females biting at 30 feet are intermediate in age between those at ground level and at 90 feet, but are probably closer to the latter. Females at 60 feet are so similar in age to those at 90 feet that it seems justifiable to combine results for the two levels. If this is done, the proportion of nullipars biting at night can be seen to decrease in a regular fashion from ground level to 120 feet. Females biting at ground level during

the day are almost identical in age to those biting at 60 feet at night, and are therefore significantly older than those at ground level at night. If the day and night are regarded as integral periods, it may be said that by day, when biting activity is very low, a higher proportion of biting pars is found at ground level and that by night the highest proportion is found above the canopy and the lowest at ground level.

TABLE III.—*The significance and frequency of inter-level differences in nulliparous rate of* Mansonia fuscopennata

		Youngest				Oldest
	Level and time	Ground (night)	30	90	60	Ground (day)
Oldest	120	S (12)	<0·02 (10)	S (10)	<0·05 (9)	<0·02 (8)
	Ground (day)	S (12)	>0·3 (8)	>0·7 (5)	>0·95 (9)	
	60	S (9)	>0·5 (8)	>0·75 (6)		
	90	S (11)	>0·5 (9)			
Youngest	30	<0·02 (8)				

Data for 30, 60, 90 and 120 feet refer only to the night hours (18–06).

Figures in each cell indicate the statistical significance and (in brackets) the frequency of occurrence of the differences by which the average age of a level-group in the left-hand column exceeded that of a group in the top line of the same column. Values of P are for one degree of freedom derived from χ^2 tests on inter-level differences, S denoting a value less than 0·001. The frequencies given record the number of catches out of 13 in which the difference observed was in the stated direction.

It has already been remarked that, above the canopy, biting activity is largely confined to the two peak periods, whereas this is not so at ground level. It follows that the nulliparous rates recorded for 120 feet and 90 feet in Table II are determined largely by females biting at 18–19 hours and 05–06 hours, whereas the rate for ground level is determined also by substantial numbers of mosquitoes that bite in the intervening period.

It is therefore meaningful to analyse inter-level differences at these two times when biting was greatest at all levels. If this is done (Table IV), two interesting facts emerge. First, there are significant differences between the age of females in the sunset and sunrise peaks at 90 feet, at ground level, and perhaps also at 120 feet. Furthermore, nulliparous rates for the intervening night hours (*i.e.* 19–05) lie between the sunset and sunrise values at all levels except 60 feet, thus indicating that the differences observed reflect trends occurring throughout the night. Second, the direction of these trends is different above and below the canopy. Above the canopy females become older as the night progresses ; below it they become younger. This means that inter-level differences are relatively small at 18–19 hours, when they are statistically significant only between 120 and 90 feet ($P < 0·01$) and between 120 feet and ground

level ($P < 0{\cdot}02$); in the 05–06 period, however, three and possibly four inter-level differences are significant, namely: 120 feet and ground level ($P < 0{\cdot}001$), 90 feet and ground level ($P < 0{\cdot}001$), above and below the canopy (see groupings in Table IV) ($P < 0{\cdot}001$), and 90 and 30 feet ($P < 0{\cdot}05$). It must be remembered that the small size of some samples from the sunrise peak reduces the significance of inter-level differences there. In spite of this, however, these analyses confirm that the biting populations above and below the canopy are changing in age in different ways, and furthermore that, during the hour when biting activity is greatest at all levels, age differences between them are smallest. At 90 and 120 feet, where about 70–80 per cent. of females bite in the sunset and sunrise hours, these differences find simple expression in the form of the biting-cycle, by slightly affecting the relative heights of the two peaks. At ground level, however, where only 24 per cent. of night-biting females are caught at these two times, the age-composition of those biting in the intervening hours will influence the biting-cycle to a greater extent, and therefore merits further examination.

TABLE IV.—*Differences in nulliparous rate of* Mansonia fuscopennata *biting at sunset and sunrise*

Level (feet)	Percentage nulliparous			Comparison of constitution of sunrise and sunset peaks; values of P
	Sunset 18–19	Night 19–05	Sunrise 05–06	
120	59·4	52·9	50·5	$<0{\cdot}05$
90	66·9	59·0	41·3	S
60	65·1	60·1	61·9	$>0{\cdot}75$
30	60·0	66·9	68·0	$>0{\cdot}30$
Ground	69·1	73·7	77·5	S
Above canopy (120 + 90)	63·8	56·6	48·8	S
Below canopy (30 + ground)	66·9	72·9	75·9	$<0{\cdot}05$

The biting-cycles of nulliparous and parous females at ground level are shown in figure 1. Before discussing in detail the patterns they show, it should first be remarked that almost every fluctuation in the biting activity of the nullipars has its counterpart in that of the pars.

The difference already noted between the age-composition of females biting in the sunset and sunrise peaks is clearly revealed in figure 1. The contribution of the parous element of the population is to accentuate the sunset peak and to reduce the relative height of the sunrise one. In fact no sunrise peak can be discerned in the biting-cycle of pars, although a peak does occur at 03–04 hours. Thus we encounter here a difference in the form of the biting-cycle which can be ascribed wholly to the relative frequencies of nulliparous and parous mosquitoes. It should be emphasised, however, that this difference exists only at ground level. The relative excess of pars at higher levels in the sunset peak more than compensates for it, and the biting-cycles for nullipars and pars at all levels combined are almost identical (fig. 2).

Whereas the peaks at sunset and sunrise are typical features of the biting-cycle of *M. fuscopennata* in a variety of forest habitats around Entebbe (Part VII), the two subsidiary peaks which occur at 22–23 and 03–04 hours in the ground-level sample at Mpanga (fig. 1) are apparently peculiar to this series of 13 catches. In the complete series of 40 catches at this site (Part VII, p. 319), these peaks cannot be discerned. The main interest which attaches to them in the present study concerns the possibility that either may represent the sudden arrival of a group of females which is homogeneous in age.

Examination of the composition of these peaks can be confined to the ground-level sample. The first peak is discernible only at ground level; the second is possibly represented amongst pars at 30 feet but not at any other level.

The raw data reveal that the first peak was the result of unusually high catches on two nights (23rd February and 6th April, 1959), and that the second peak was caused by unusually high catches on three nights (29th December, 1958, 2nd and 23rd February, 1959). In all of these catches both nullipars and pars showed a noticeable increase in biting activity in the hours corresponding to these peaks. In one catch (23rd February, 1959) both nullipars and pars achieved their highest totals for the whole catch in the hour of the first subsidiary peak. The nulliparous rates of the samples taken during the hours of the two small peaks were in all cases slightly lower than those for females arriving during the rest of the 24 hours combined. Thus it may be concluded that these subsidiary peaks cannot have been caused by the arrival of an emergence group, and that the factors responsible for them affected both age-groups in a similar way.

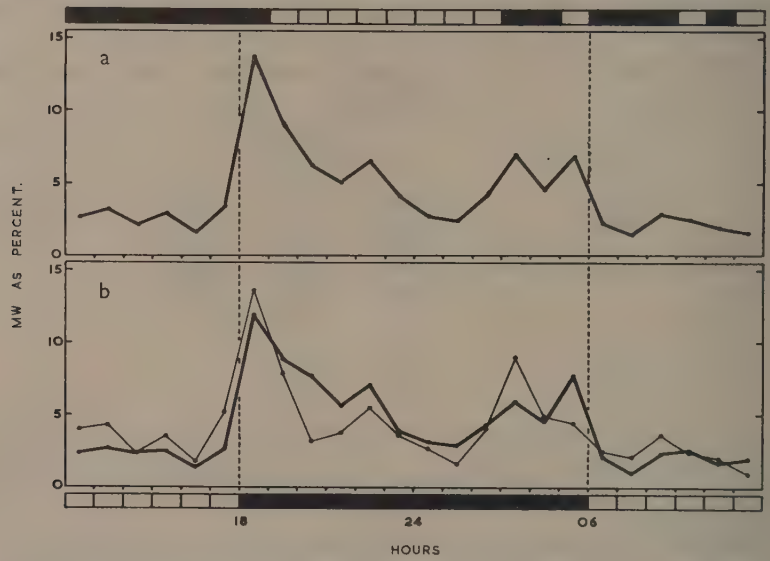

FIG. 1.—*Mansonia fuscopennata*. The biting-cycles of nulliparous and parous females at ground level. *a*, All females combined (total 1844). *b*, Thick line—nullipars (1298); thin line—pars (546).

The horizontal time scale at the top of the figures is blackened in hours when pars exceed nullipars on a percentage basis.

During another catch (27th October, 1958) the biting activity between 23 and 06 hours was unusually high at all levels except 120 feet. Although the average age of the total sample was very low (the nulliparous rate was 82·6 per cent.), it is noteworthy that on this night also both nullipars and pars showed the same anomalous pattern of biting activity.

These atypical catches showed no obvious relation to the age or exposure of the moon.

Brief mention should be made here of an age-analysis carried out on 332 males of *M. fuscopennata* caught in light-traps on the tower (Part VI, p. 306). Males were classified according to three characters: (1) the degree of rotation of the hypopygia; (2) the presence on them of hydrachnid mites (Gillett, 1957); and (3) the presence of scars vacated by these mites (*see* Marshall and Staley, 1929). The first character is well known to be reliable for recognising newly-emerged males. The validity of the second and third characters has recently been investigated in females of *M. fuscopennata*

(Corbet, 1959*b*, 1960*a*) although not in males. In females, more than 97 per cent. of individuals bearing hydrachnid mites are nulliparous, whereas more than 85 per cent. of those with vacant scars are parous. The most that can be said for males at present is that those with mites must on the whole be younger than those with vacant scars.

The analysis referred to above was undertaken to compare the ages of males flying before and after midnight, respectively. Although no significant differences were recorded, it is of interest to note that the temporal incidence of all three characters was consistent with the assumption that the younger males were those flying after midnight. This result is of interest in view of the finding that younger females of this species bite later in the night.

Similar age-analyses conducted on males and females of other species of *Mansonia* gave no indication of a non-random distribution of age-groups.

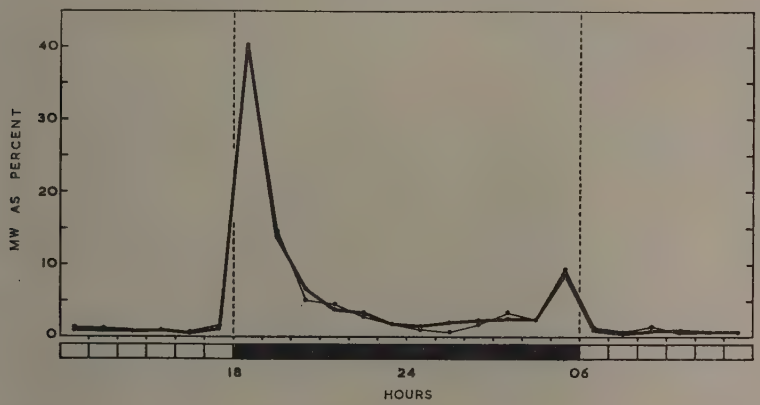

Fig. 2.—*Mansonia fuscopennata*. The biting-cycles of nulliparous and parous females ; all levels combined. Thick line—nullipars (total 2845) ; thin line—pars (1556).

Aedes apicoargenteus

Data for this species are limited to records for 188 mosquitoes from 8 catches, and are too few to merit analysis. It is noteworthy, however, that only 22·3 per cent. were nulliparous, and that in some catches no nullipars were taken. No clear-cut differences in biting activity could be discerned between nullipars and pars.

Culex annulioris

Twenty-six females from six catches were dissected, 11 being nulliparous. All were caught at ground level and revealed no obvious differences in biting times of nullipars and pars.

Discussion

The results described here agree with those of certain other workers (Gillett, 1957 ; Gillies, 1957) in showing that the characteristic form of the biting-cycle in a mosquito is not related to the age-composition of the biting population (*see* fig. 2). The present study has in fact demonstrated that the factors which cause minor as well as major fluctuations in biting intensity act on both nullipars and pars of *M. fuscopennata* in essentially the same way.

A respect in which the present data resemble those obtained by workers investigating other groups of biting Diptera is that they reveal small but consistent changes in the proportions of nullipars and pars which are correlated with different times of day. In *M. fuscopennata* it has also been shown that these changes can be related to the height above ground at which biting occurs.

From an epidemiological point of view, the results of all these studies support the general conclusion that, although the likelihood of a host receiving an infective bite (from a parous female) may fluctuate according to time and level, it will nevertheless remain a possibility throughout the period during which biting occurs. At Mpanga there is no time or level at which only nullipars of *M. fuscopennata* bite, and thus, if this mosquito were a vector of disease, there would be no " safe " period during which all the females biting were doing so for the first time. The changes in nulliparous rate which have been observed in this species are not of sufficient magnitude to modify the statement that the chances of infection will be greatest when the general biting-cycle shows that the largest numbers of mosquitoes are biting.

The close similarity between the biting-cycles of nullipars and pars of *M. fuscopennata* necessitates a revision of the general hypothesis of Lumsden (1952) advanced to explain the form of mosquito biting-cycles on the basis of age-groups. There are, however, certain steps in Lumsden's argument which, if considered independently, may help to explain facts recorded in the present paper.

Lumsden pointed out that in species with extensive breeding places, which may therefore produce large adult populations, there would be little necessity for individual adults to be long-lived or to undergo repeated ovarian cycles. In species with circumscribed breeding places, however, populations would be small and the need for longevity in the adult correspondingly greater. At Mpanga, observations made on *M. fuscopennata* and *Ae. apicoargenteus* support this thesis. *M. fuscopennata*, an abundant mosquito breeding in grass swamps (Gillett, 1946), showed an overall nulliparous rate of 64·6 per cent., whereas *Ae. apicoargenteus*, a breeder in small-containers (Dunn, 1926), which was much less common, showed a rate of only 22·3 per cent.

Concerning the changes in average age of *M. fuscopennata* which occur during the night, it should be mentioned that both Lumsden (1952) and Colless (1956) have suggested that younger females may bite more frequently late in the night, a phenomenon which has been observed below the canopy at Mpanga. Lumsden also drew attention to the important differences in the biological events that precede the act of biting between nullipars and pars. Thus, females biting for the first time will be those which have just completed the period of inactivity following emergence, and perhaps, though not necessarily, have just mated. On the other hand, the main event preceding biting in parous females will be oviposition.

At present there are still too many unknown factors in the biology of *M. fuscopennata* for these ideas to be critically applied to the present data, and in any case it must be remembered that the differences in biting behaviour between nullipars and pars are of a relatively minor order. However, the possibility should be noted that, if a substantial number of newly-parous females come to bite directly from oviposition sites, then they may perhaps be expected to bite more frequently at the margins of forest than inside, and further, if some are able to bite during the same night that they have oviposited (*see* Haddow and Gillett, 1958), then pars will be proportionately more numerous at marginal sites later in the night.

It is felt that considerations such as these may subsequently help to explain the changes in average age of females biting above and below the canopy at Mpanga. It must be emphasised, however, that these rationalisations are of a very tentative nature, and it is clear that these questions need to be pursued much further before the trends observed can be understood Contemporaneous age-analyses of populations, biting in different situations at ground level inside and outside forest, might be informative.

Acknowledgments

I am much indebted to Dr. A. J. Haddow for making available to me the sorted material from his catches, and I have derived great benefit from discussions with Drs. J. D. Gillett and M. T. Gillies.

Summary

1. The age-composition of mosquitoes biting at different times and levels was investigated at Mpanga Forest. The species studied in detail, *Mansonia fuscopennata*, has a biphasic biting-cycle at all levels, and is therefore well suited for testing the hypothesis that the pattern of the biting-cycle is determined by differences in the behaviour of nullipars and pars.

2. Female mosquitoes were classified on ovarian characters as either nulliparous or parous, and were grouped according to time and level. Samples were taken at five levels, from the ground to a height of 120 feet, about 50 feet above the canopy. Data comprised records for 4401 mosquitoes, obtained in thirteen 24-hour catches made by Haddow.

3. The biting-cycles of nullipars and pars were closely similar at each level, and were almost identical when all levels were combined. In nearly every case, both major and minor fluctuations in biting intensity were reproduced in the biting-cycles of both age-groups. Thus the factors responsible for these fluctuations must affect nullipars and pars in essentially the same way, and the characteristic form of the biting-cycle is not the result of differential activity in these two sections of the population.

4. Were *M. fuscopennata* a vector of disease, there would accordingly be no " safe " period when only nullipars were biting. The time when the chances of receiving infective bites from this species would be greatest can be determined directly from inspection of the general biting-cycle.

5. Although the biting-cycles of nullipars and pars are closely similar, significant and consistent differences were discerned in the average age of females biting during the night at different levels. Young females were most numerous at ground level, and older ones at 120 feet, and when inter-level differences were significant, average age increased according to the height above ground. At ground level, females biting during the night were younger than those biting there during the day.

6. The age-composition of females biting above and below the canopy changed during the night. Above the canopy the average age increased from sunset to sunrise, whereas below the canopy it decreased. Thus, in the hour after sunset, when biting activity was greatest at all levels, age differences between levels were least ; and thereafter these differences increased until sunrise. In the whole 24-hour period, females were youngest in the hour before sunrise at ground level, and oldest in the same hour at 90 feet.

7. The differences in average age recorded at different times and levels are possibly an expression of the events which precede biting in nullipars and pars respectively.

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

IX. OBSERVATIONS ON LEPIDOPTERA (RHOPALOCERA)

By T. H. E. Jackson

(*Kapretwa, Kitale*)

Two African collectors, occupied solely in collecting Lepidoptera, were stationed on the tower for the period March to November 1959, inclusive.

Collections were made daily and at all times during the day but, owing to the distance involved, the writer could make only a few personal visits and no really detailed data can be given as regards flight periodicity for the various species. It appears that flight was much the same as at ground level for diurnal Lepidoptera, *i.e.* from 0930 to 1400 hours, with a peak from 1130 to 1300 hours, and thereafter a pause during the hottest hours of the day, followed by a further, lesser, flight period from 1500 to 1630 hours; the hours (East African Standard Time) are approximate. They are roughly 50 minutes ahead of sun-time, which is used in the other papers in this series.

There is considerable movement of Lycaenidae, Lipteninae (*sens.* Aurivillius, 1925) in the late afternoon and this was apparent also on the tower.

As regards height, the main concentration was around the 60-foot level, *i.e.* in and below the main canopy, with some considerable movement above the canopy, and virtually none below the 30-foot (understorey) level. The main interest from this angle centres round the height preferences of individual species, and this probably explains the occurrence of so many species not previously taken in this area. A few examples are :—

Teratoneura isabellae congoensis Stempffer—only above the canopy.

Liptena congoana	Hawker-Smith	at about the 60-foot level.
Eresina fontainei	Stempffer	
jacksoni	Stempffer	
bergeri	Stempffer	
crola	Talbot	
Toxochitona bilinea	Talbot	
Epitola mengoensis	Bethune-Baker	

Flight was regulated, as at ground level, by sunlight, and in dull cloudy weather ceased altogether.

The collection was of great taxonomic interest since a number of species, previously represented by only a few examples and often of only one sex, may now be described.

A list of species taken is given below, and certain apparent anomalies can be explained as follows :

Papilionidae — The absence from the collections of this family, members of which were often seen flying high up in the canopy, is purely due to technical difficulties. In collecting at all levels on the tower, the net had to be fixed to a long pole and it was impossible to catch a fast-flying insect such as a *Papilio*.

Danaidae, Pieridae, Satyridae — The species in these families are well known and were not collected. The Satyridae occur only at ground level.

Nymphalidae — Traps were placed at certain levels on the tower and baited with fermented banana, and this accounts for the inclusion in the list of some normally ground-level genera such as *Euphaedra*, *Euryphene* and *Diestogyna*. The genus *Charaxes* is well represented, and all those mentioned in the list were taken in the traps. One species was new for this area. They are often seen flying in and above the canopy.

The Lycaenidae, as expected, provided the greatest interest in the investigation. No less than 78 species were taken from the tower, the majority belonging to the sub-group Lipteninae (*sens.* Aurivillius, 1925). The eggs in this group are laid on the tree-trunks, usually among ants (*Crematogaster*), and the larvae feed on lichens or on honey-dew left or provided by the ants. Both larvae and pupae are cryptically coloured and ornamented to represent the lichen on the bark. They are, therefore, essentially forest insects. A large number of those taken of this group were in very fresh condition and it is thought that, after emergence, the females ascend to the canopy to feed and to mate and that the males await them in and around this area. This may account for the general habit of the sub-family of living at great heights.

A system of starring has been adopted in the list as follows :

* Not previously known from Uganda.

** Not previously taken in the general area of the Mpanga Forest, including all nearby forest areas.

*** Previously known from a few examples only, often of one sex only.

Note : For the purposes of this list the arrangement of families is that of Aurivillius (1925).

PAPILIONIDAE

Nil

PIERIDAE

Nil

DANAIDAE

Nil

SATYRIDAE

Mycalesis aurivillii Butler

NYMPHALIDAE

Charaxes pollux pollux Cramer
brutus brutus Cramer
eudoxus mechowi Rothschild
numenes numenes Hewitson
tiridates tiridates Cramer
bipunctatus Rothschild
** *imperialis imperialis* Butler
eupale latimargo Joicey and Talbot
lichas bebra Rothschild
anticlea adusta Rothschild
etheocles carpenteri Poulton
Euptera elabontas mweruensis Neave
Euryphene carshena Hewitson
Euphaedra ruspina Hewitson
uganda uganda Aurivillius
preussi olivacea Grünberg
Diestogyna saphirina Karsch
Pseudacraea eurytus Linnaeus (forms)

NYMPHALIDAE

Asterope occidentalium Mabille
boisduvali omissa Rothschild
Mesoxantha ethosea Drury
Eurytela hiarbas Drury
Apaturopsis cleocharis Hewitson
Precis westermanni Westwood

ACRAEIDAE

Bematistes tellus eumelis Jordan
epaea paragea Grose-Smith
poggei nelsoni Smith and Kirby
Acraea orina orineta Eltringham
penelope Staudinger
quirinalis Grose-Smith
terpsichore Linnaeus
althoffi Dewitz
bonasia Fabricius

RIODINIDAE

Libythea labdaca Fabricius

LYCAENIDAE

Lachnocnema bibulus Fabricius
***Aslauga lamborni* Bethune-Baker
Telipna erica ugandae Bethune-Baker
nyanza Neave
carnuta parva Kirby
Pentila prodita connectens Hulstaert
tachyroides Dewitz
Ornipholidotos overlaeti Stempffer
kirbyi Aurivillius
** *katangae* Stempffer
ugandae Stempffer
ntebi Bethune-Baker
Mimacraea krausei poultoni Neave
Mimeresia favillacea griseata Talbot
dinora discirubra Talbot
neavei Joicey and Talbot
***Pseuderesia eleaza* ssp. nov.
sp. nov.
Citrinophila erastus pallida Hawker-Smith
Larinopoda tera Hewitson
***Liptena congoana* Hawker-Smith
praestans congoensis Schultze and Aurivillius
xanthstola xantha Smith and Kirby
ilma ilma Hewitson
hapale Talbot
sp. nov.
Micropentila brunnea Kirby
*** sp. nov.
***Eresina bergeri* Stempffer
*** *crola* Talbot
** *jacksoni* Stempffer
* *fontainei* Stempffer

LYCAENIDAE

******Toxochitona bilinea* Talbot**
****Teratoneura isabellae congoensis* Stempffer**
Epitolina catori ssp. nov.
dispar melissa H. Druce
Epitola doleta entebbeana Bethune-Baker
carpenteri Bethune-Baker
catuna Kirby
******** *mengoensis* Bethune-Baker
Hewitsonia kirbyi intermedia Joicey and Talbot
Megalopalpus zymna simplex Röber
Hypokopelates eleala ugandae Talbot
Pilodeudorix diyllus orientalis Stempffer
caerulea caerulea H. Druce
camerona Plötz
Virachola odana H. Druce
dinomenes Grose-Smith
Oxylides faunus albata Aurivillius
Hypolycaena lebona Hewitson
liara liara H. Druce
hatita ugandae Sharpe
philippus Fabricius
Tanuetheira timon orientius Hulstaert
Iolaphilus poecilaon Riley
Philiolaus parasilanus divaricatus Riley
Epamera pollux albocaerulea Riley
hemicyanus hemicyanus Sharpe
******Myrina sharpei* Bethune-Baker**
Aphnaeus orcas hollandi Butler
****** *argyrocyclus* Holland
****** *jefferyi* Hawker-Smith
Lipaphnaeus loxura Rebel
Axiocerses bambana Grose-Smith
Spindasis crustaria Holland
Anthene larydas Cramer
liodes Hewitson
alberta Bethune-Baker
schoutedeni Hulstaert
musagetes Holland
****** *levis grisea* Talbot
Triclema lamias Hewitson
hades Bethune-Baker
Oboronia punctata Dewitz
Castalius margaritaceus Sharpe
Azanus natalensis Trimen
isis Drury
Spalgis lemolea H. Druce

HESPERIIDAE

Celaenorrhinus galenus intermixtus Aurivillius
Eagris lucetia Hewitson
Netrobalane canopus Trimen
Spialia rebeli Higgins

HESPERIIDAE

Ceratrichia argyrosticta enta Evans
Pardaleodes bule Holland
Acleros mackenii Trimen
Hypoleucis ophiusa ophir Evans
Meza cybeutes pallida Holland
Chondrolepis niveicornis Plötz
Pteroteinon caenira Hewitson

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

X. OBSERVATIONS ON SPHINGIDAE (LEPIDOPTERA)

By Philip S. Corbet

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Introduction

In the course of the work on the tower in Mpanga Forest (*see* Part I), records were kept of the Sphingidae caught in five mercury-vapour light-traps. These traps (Part VI, p. 302) were placed on the tower at ground level, and at heights of 30, 60, 90 and 120 feet. The tower passed through the lower and upper limits of the forest canopy at about 50 and 70 feet, respectively. Each trap emitted light as a narrow horizontal beam which thus minimised interference between adjacent levels. The five traps were operated simultaneously at all levels, from an hour before sunset until an hour after sunrise (17–07 hours), and the catch in each was examined hourly. Only in the first three catches (between 25th September and 10th October, 1958) were Sphingidae recorded; subsequently, wire screens were placed around the traps to prevent the entry of large insects, and thus they were seldom caught. The present records are of interest in that they provide information on the vertical distribution of Sphingidae in and above forest at night.

It is a pleasure to thank Mr. John Bowden, Senior Entomologist, Agricultural Department, Uganda, for giving me access to the insect collection at Kawanda Agricultural Research Station, and for assisting me with the identification of some of the species.

Results

In the list of captures below, the level is recorded first (in heavy type), and is followed by the time at the beginning of the one-hour period during which the insect was caught; and the number taken is given in brackets when it is more than one. Thus "**120** : 19(2)" denotes the capture of two specimens at 120 feet between 19 and 20 hours. Species are listed in alphabetical order, and the nomenclature is that of Hering *in* Seitz (1930).

Basiothea medea Fab. **90** : 21 ; 22.
Coelonia fulvinotata Butl. **0** : 21(2) ; **30** : 21 ; **60** : 22 ; **90** : 23 ; **120** : 23 ; 00.
Euchloron megaera L. **120** : 19.
Herse convolvuli L. **90** : 22 ; **120** : 21(2) ; 22(2).
Hippotion celerio L. **0** : 03.
Nephele aequivalens Walk. **60** : 01 ; 02 ; **90** : 19 ; 01 ; 02 ; 03(2) ; **120** : 04(2).
N. comma Hopffr. **90** : 23 ; 00.
N. rosae Butl. **0** : 03 ; **120** : 21.
Platysphinx constrigilis Walk. **120** : 22.
Polyptichus carteri Butl. **0** : 03 ; **60** : 21.
P. orthographus R. and J. **90** : 23 ; 02.
P. spurelli Roths. **30** : 22.
Pseudoclanis postica Walk. **0** : 00 ; **30** : 23.
Temnora crenulata Roths. **60** : 00.
T. fumosa Walk. **120** : 20.
T. scitula Holl. **60** : 22 ; **90** : 00.

T. sp. nr. *crenulata* Roths. **0** : 01 ; **90** : 01(2) ; **120** : 00.
T. sp. nr. *sardanus* Walk. **120** : 02.
Temnora sp. **60** : 19.
Theretra jugurtha Bsdv. **0** : 22 ; **90** : 23 ; **120** : 02.
T. orpheus H. S. **60** : 10 ; **90** : 22 ; **120** : 00 ; 04.

TABLE I.—*Captures of Sphingidae at different levels*

	Height in feet				
	0	30	60	90	120
Number of individuals	8	3	9	18	18
Number of species	7	3	8	10	12
Number of species taken only at one level	1	1	2	3	4

These records show that Sphingidae were caught more or less throughout the period 19–06 hours, but that about 57 per cent. of the specimens were taken between 21 and 01 hours. An analysis of captures according to level (Table I) reveals that more species and more individuals per trap were caught above the canopy than below it.

This difference may simply be an expression of the effectiveness of the several traps, since those surrounded by foliage would presumably sample only a small area. Nevertheless, these records indicate that a variety of species of sphingids may be active over forest at night, and that they frequently fly at heights of up to 120 feet.

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

XI. OBSERVATIONS ON COLEOPTERA

By Keith W. Brown

(*Forest Department, Uganda*)

Between October, 1958 and January, 1959, I had the opportunity to examine a number of light-trap catches taken on the Virus Research Institute tower situated in the Mpanga Forest (*see* Part I). From these I obtained numerous Coleoptera belonging to families of known silvicultural importance. Most of these specimens have now been identified and are listed at the end of this note.

Mpanga Forest has been an intensively collected area since 1953: a total of about 48 man-months (each consisting of 28 man-days) have been spent there by trained collectors, and a large proportion of the Department's Reference Collection of Forest Insects originates therefrom. In view of this it is interesting to note that more than half of the species identified from the light-traps are new records for this forest, and this indicates the considerable value of light-trap collections as a supplement to normal methods of collecting xylophagous insects. It is, however, also apparent that they should not be considered an effective substitute for the normal methods since, for example, out of a total of 78 species of Cerambycidae recorded previously from Mpanga, only 5 appeared in or at the light-traps. Obviously light-traps will produce a poor representation of families which are primarily diurnal, as are the Cerambycidae, but they may also fail to catch examples of important species of crepuscular and nocturnal groups which may be taken by other methods.

On two occasions (October 23rd and 30th, 1958) it was possible to analyse the catches according to time and height above ground and this analysis gave some interesting indications of flight habits, but being based on only two nights' catches it should be stressed that they are merely indications.

Firstly, the activity peak of the Ambrosia Beetles (*i.e.* all the Platypodidae taken and the genus *Xyleborus* of the Scolytidae) is between one hour before sunset and one hour after. This is in agreement with observations made on the West Coast by Webb and Jones (1958).

Secondly, there appears to be a tendency for some vertical stratification, with 97 per cent. of the *Scolytoplatypus* being taken at 90 feet and 120 feet and 76 per cent. of the *Xyleborus* at 60 feet and below.

Thirdly, activity in the Brenthidae appears to continue until midnight or later. This family appears to be largely nocturnal, the species appearing in the traps almost doubling the records for this family at Mpanga.

It is hoped to test the validity of these observations more thoroughly when trapping is resumed at a new site.

Coleoptera caught in M.V. light-traps at Mpanga, 1958–59

Anobiidae

Ptilinus senegalensis Pic.

Anthribidae

* Gen. et sp. incog. (1)

* Gen. et sp. incog.(2)

BOSTRYCHIDAE

* *Amintinus gardneri* Vrydagh (sp. nov.)
Sinoxylon brazzai Lesne

BRENTHIDAE

* *Adidactus* sp. indet.
* *Allogogus* sp. indet.
* *Bolbocephalus opacus* Klbe.
* *Cerobates debilis* Thoms.
* sp. aff. *fortunatus* Klbe.
* sp. aff. *punctulatus* Senna
* sp. indet.
* *Cormopus* sp. aff. *simplex* Klne.
Isoceocephalus rufescens Thoms.
* *Jonthocerus conradti* Klbe.
Megalosebus ? comparabilis Klbe.
* sp. not in B.M.
Oncodemerus costipennis Senna
* *Rhytidopterus* sp. indet.
* *Schizoadidactus tibialis* Klne.
* *Usambius conradti* Klbe.

BUPRESTIDAE

Agrilus sp. indet. (1)
sp. indet. (2)

CERAMBYCIDAE

CERAMBYCINAE

Alloeme rubra Thoms.
* Gen. aff. *Anisogaster*

LAMIINAE

Bangalia nebulosa Qued.
* *Eunidia flavovittata* Breun.
* spp. not in B.M.
* *Graciella zanzibarica* Jord.
* *Homelix cribratipennis* Thoms.
Moecha fasciata Aur.
Oeax lichenea Duviv.
Phrynetopsis fuscicornis Chevr.
* *Pterolophia* sp.
* *Sophronica calceata* Chevr.
* sp. aff. *striatipennis* Breun.
* sp. indet.
* Gen. et sp. incog.

CLERIDAE

* *Cardiostichus nigrogeniculatus* Kuw.
Erymanthus ? gemmatus Klug.
* *Phaeocyclonotomus* sp. not in B.M.
* *Tenerus* sp. not in B.M.

COLYDIIDAE

* *Metacerylon parallelum* Grouv.
* sp. indet.
Pubala ornatula Pope
* *Sosylus minutus* Pope

CURCULIONIDAE

* *Balaninus* sp. not in B.M.
* *Camptorhinus* sp. not in B.M.
* *Endaeus* sp. indet.
Euops togoensis Faust.
Haplocorynus deceptor Marshall
*?*Mecistocerus* sp.
* *Rhadinomerus* sp. indet.

ELATERIDAE

* *Craspedostethus* sp. indet.
* *Elasmosomus* sp. indet.
* Gen. aff *Rhinopsephus* sp. indet.

LYMEXYLIDAE

Atractocerus brevicornis L.

PLATYPODIDAE

Doliopygus chapuisi Duv.
opifex Samp.
serratus Strohm.
spp. indet.
Periomatus camerunus Strohm.
sp. indet.
Platypus hintzi Schauf.
spp. indet.
Symmerus tuberculatus Chap.

SCOLYTIDAE

* *Ctonoxylon nodosum* Egg.
* *Hylesinopsis dubius* Egg.
* *Hypothenemus* sp.
* *Mimips biconicus* Schedl
* *euphorbiae* Schedl
* *katangensis* Egg.
* *quadrituberculatus* Schedl
* *Polygraphus natalensis* Egg.
Premnobius cavipennis Eichh.
* *Scolytoplatypus africanus* Egg.
spp. indet.
Xyleborus confusus Eichh.
eichhoffi Schrein
ferrugineus F.
mascarensis Eichh.
* *ricini* Egg
* *rothkirki* Egg.
testaceus Walk.
* *torquatus* Eichh.
Xyleborus (*Premnobius*) *sexspinosus* Egg.

* Denotes a new record for this forest.
B.M. denotes British Museum (Nat. Hist.), London

ENTOMOLOGICAL STUDIES FROM A HIGH TOWER IN MPANGA FOREST, UGANDA

XII. OBSERVATIONS ON EPHEMEROPTERA, ODONATA AND SOME OTHER ORDERS

By Philip S. Corbet

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Introduction

During the programme of work designed to study the activity and vertical distribution of biting Diptera in Mpanga Forest, casual observations were made on certain other orders of insects. These observations are included in the present series of papers since very little is known about the ecology of some of the groups concerned, and even less about their habits in a forest environment. The data are presented either as occurrence records, or as brief notes on habits or vertical distribution.

A description of the forest, and of the tower on which many of the observations were made, has been given in the introductory paper of this series (Part I). Certain additional facts should be mentioned here : the tower stood about 70 yards from the forest margin, and passed through the lower and upper limits of the uneven canopy at heights of about 50 and 70 feet, respectively. A small, well-shaded, forest stream passed within about 30 yards of the base of the tower. This stream was fed by a spring in the forest nearby ; it was freely flowing in parts, and was typical of other streams in the forest at which collections were made. In these streams, there were some places where the turbid water was almost stationary over a bottom of leaf litter and fine silt, and others where the flow was sufficient to generate surface ripples over a bottom of coarse sand.

With the exception of the Odonata, and unless otherwise stated, all insects were collected in September and October, 1958, in mercury-vapour light-traps which were operated on the tower at ground level, 30 feet, 60 feet, 90 feet and 120 feet (Part VI). Owing to pressure of other work, collections could not be made after these months. Material was usually combined from all levels and all hours, but on a few occasions separate records were kept. Simple occurrence records are derived from the combined collections. The times recorded refer to " catch-time " in which the exact time of sunset is designated as 1800 hours (Lumsden, 1952).

Ephemeroptera

All specimens were imagines.

Baëtidae

Procloëon rhodesiae (Barnard). 6 males, 1 female.

Leptophlebiidae

Adenophlebia burgeoni Navás. 7 males, 1 female. Also 1 male at 120 feet, 05–06 hours, 10.i.59.

Adenophlebioides ornatus (Ulmer). 6 males, 1 female. Also 2 males at 120 feet, 05–06 hours, 26.ix.59. Swarms were observed at 6–10 feet above the top platform on the tower (120 feet) on two mornings, each time between 0530 and 0535. Each swarm comprised two or three males, rising and falling in the typical dancing flight From such swarms 1 male was caught on 10.i.59 and 2 males on 13.i.59.

Odonata

Unless otherwise stated, specimens were adult and were collected over streams inside the forest during the day.

Platycnemididae

Platycnemis congolensis Martin.

Coenagrionidae

Pseudagrion serrulatum Karsch.

P. kibalense Longfield.

Enallagma longfieldae Fraser.

Calopterygidae

Umma saphirina Forster. Adults of both sexes frequent paths or small gaps in the herb layer, where they settle on leaves in the sunlight. Two males were seen mutually displaying near a stream at a height of 15–20 feet in a shaft of sunlight penetrating the canopy. Adults are seldom seen near water during the day.

Chlorocyphidae

Chlorocypha straeleni Fraser.

Gomphidae

Notogomphus lujai Schouteden. One mature male taken in a light-trap at 30 feet at 18–19 hours.

N. sp. Larvae found amongst leaf litter in a stream.

Paragomphus sp. probably *cognatus* Rambur. Larvae found in a stream, in a stretch where the flow was relatively fast.

Aeshnidae

Acanthagyna bullata Karsch. A mature male found resting in heavy shade near ground level in daytime ; a female seen ovipositing at about 16 hours on the vertical clay-bank of a shaded ditch about 6 inches above the water surface ; several males hawking vigorously along the forest margin and in a nearby banana plantation at 17–18 hours.

A. villosa Grünberg. A mature male hawking along the forest margin at 1805 ; a mature male caught at 120 feet while hawking actively above the forest canopy at 1817 hours.

A. sp. probably *villosa*. An adult seen flying near the tower at 90 feet at about 1730 ; an adult seen flying rapidly over the tower at about 140 feet at 0542. Larvae found in a stream.

Corduliidae

Phyllomacromia sylvatica Fraser. Larvae found in a stream.

Libellulidae

Tetrathemis corduliformis Longfield. Males frequent sunny situations in the herb layer, where they settle on leaves near the ground.

Notiothemis robertsi Fraser. Resembles *T. corduliformis* in habits. A mature male taken in a light-trap at ground level at 14-15 hours.

Micromacromia camerunica Karsch. Adults frequent sunny paths in forest during the day. A pair *in copula* settled on a bush at a height of about 6 feet at 14 hours.

Orthetrum hintzi Schmidt. A mature male taken in a light-trap at 30 feet at 18–19 hours.

O. julia Kirby. The commonest libellulid to be encountered in sunny situations on the forest floor. A mature male taken in a light-trap at 60 ft. at 21–22 hours ; and two mature females probably of this species in light-traps at ground level at 00–01 hours, and at 30 feet at 20–21 hours. Larvae found in a stream amongst mud and leaf litter.

O. stemmale falsum Longfield. A mature female taken at ground level in forest.

LIBELLULIDAE

Hadrothemis camarensis Karsch. The only adults to be found were mature females which had been drowned in bamboo sections put out for mosquito-breeding surveys (Part IV, p. 282). These had presumably been ovipositing there, since larvae (from which adults were reared) were found in about 3 per cent. of bamboos at ground level, and also in a few on the tower up to 30 feet. It is likely that ovipositing females were drowned because the small internal diameter of the bamboo sections prevented their flying out.

H. infesta Karsch. Four mature males taken at ground level in forest.

Rhyothemis fenestrina (Rambur). On 17.ix.58 about fifty adults were seen to form a swarm-like group over the forest canopy at about 100 feet at about 15 hours. Such aggregations were frequently observed above the canopy in the mid-afternoon, or in mid-morning on sunny days. They were not seen at midday.

Pantala flavescens Fab. This migrant appears in large numbers in Uganda at certain well-defined times of year. At such times adults are common at Mpanga, hawking over open spaces or plantations outside the forest during the day and at sunset, and also high above the canopy during the day. Systematic directional movements can sometimes be discerned above the canopy.

Aethriamanta rezia Kirby. Adults, usually with immature colouring, were frequently seen perching on branches or leaves projecting from the top of the canopy.

ORTHOPTERA

BLATTIDAE

Gyna gloriosa (Stal). Adults were taken at light at 120 feet, and were also seen amongst grass in a plantation by the forest margin during the day.

TRICHOPTERA

POLYCENTROPIDIDAE

Dipseudopsis africana Ulmer.

D. capensis Walker.

HYDROPSYCHIDAE

Macronema capense var. *signatum* Walker. Adults were commonly taken at mercury-vapour light. During two catches, all males and females were recorded, the numbers of males caught at the five levels from ground level to 120 feet being 2, 1, 7, 6, 1 and of females 0, 1, 0, 1, 4. Thus both sexes were active at night, the males at all levels, and the females at least in the understorey and in and above the canopy. Males were caught in every hour from 18 to 04, except for 01 ; most were caught in the three hours after midnight. All the females except one were caught from 23 to 02. Nocturnal activity in this species appears to be greatest soon after midnight in and above the canopy.

Unidentified hydropsychid larvae occurred in a forest stream.

CALAMOCERATIDAE

Anisocentropus usambarensis Ulmer. Five to ten males were observed swarming above a forest stream, at about 1730 on 31.i.58. Males were rising and falling between the water-surface and a height of about 3 feet, in a narrow passage left between emergent aquatic plants and the ground herb layer on either bank.

LEPTOCERIDAE

Triaenodes sp. nr. *darfurica* Mosely. 1 male, 4 females.
Oecetis aganda Mosely.
O. sp. 1 female.
Leptocerus intricatus Mosely.
Adicella sylvestris Kimmins.

SERICOSTOMATIDAE

Goerodes turka Mosely.
G. darfurensis Mosely.

DIPTERA

PSYCHODIDAE

Telmatoscopus albipunctatus Say. Six taken at ground level at 17–18 hours.
Brunettia sp. One at ground level, two at 30 feet, all at 17–18 hours.

CHAOBORIDAE

Adults were looked for, and recorded according to time and level, in all of the 15 catches made with light-traps between September, 1958 and January, 1959.

Chaoborus (*Neochaoborus*) *anomalus* Edwards. Adults, females only, were taken on only four nights. The numbers caught on the various dates, and at respective ages of the moon (given in brackets) were 227 on 25.ix.58 (13 days); 71 on 16.x.58 (5 days); 1 each on 23.x.58 (12 days) and 9.i.59 (0 days). Of the 300 taken, 288 (96·0 per cent.) were caught above the canopy, and 227 (75·7 per cent) at 120 feet. This species is very common in Lake Victoria, where it exhibits a lunar periodicity of emergence (Macdonald, 1956); it is not known to breed except in large lakes (Verbeke, 1958). The sporadic occurrence of this insect, sometimes in large numbers, above the canopy at Mpanga suggests that it was carried there by winds from Lake Victoria. At Mpanga, winds from the lake predominate at all times of the day and night (Part II, p. 266), and it is perhaps significant that on 25.ix.58 the wind was recorded as blowing from the south or south-east in every hour between midday and sunset. At Mpanga, on the tower, females were caught only between 18 and 24 hours, and there was a well-marked peak of activity at 19–20 hours.

C. (*Sayomyia*) *ceratopogones* Theobald. Three adult females were taken on three nights, namely 25.ix.58 (moon-age 13 days), 23.x.58 (12 days), and 2.i.59 (23 days). Two were caught at ground level at 18–19, and one at 30 feet at 19–20 hours. Although these records are few, this vertical distribution contrasts with that of *C. anomalus* and the two other lacustrine species, and is consistent with the finding that *C. ceratopogones* breeds in the forest itself. Larvae were found in heavily-shaded ground pools near the tower in November, 1957.

C. (*S.*) *edulis* Edwards. Two adult females were taken at 120 feet at 19–20 hours on 25.ix.58 (moon-age 13 days). This species is very abundant around the shores of Lake Victoria, in which it presumably breeds (*see* Macdonald, 1956). It exhibits a lunar periodicity of emergence (Corbet, 1958).

C. (*S.*) *pallidipes* Theobald. Four adult females were taken; one at 90 feet at 19–20 hours on 16.x.58 (moon-age 5 days); one at ground level at 22–23 hours on 2.x.58 (20 days); one at 90 feet at 04–05 hours, and one at ground level at 00–01 hours on 14.xi.58 (3 days). This species breeds commonly in Lake Victoria (Macdonald, 1956).

CHIRONOMIDAE

Pentaneura (*Ablabesmyia*) *nilotica* Kieffer.
Procladius (*Procladius*) *albitalus* Freeman.
Chironomus (*Chironomus*) *chloronotus* Kieffer.
C. (*Dicrotendipes*) *chloronotus* Kieffer.
C. (*D.*) *multispinosus* Freeman.
C. (*Cryptochironomus*) *lindneri* Freeman.
Stictochironomus festivus Kieffer.
Microtendipes taitae Kieffer.
M. bifasciatus Kieffer.
Polypedilum (*Polypedilum*) *dewulfi* Goetghebuer.
P. (*P.*) *ephippium* Freeman.
P. (*P.*) *griseoguttatum* Kieffer.
P. (*P.*) *tropicum* Kieffer.

ASILIDAE

Promachus cornutus (Hobby). One male and two females taken in a light-trap at 60 feet at 19–20 hours.

DISCUSSION

Apart from observations made by the Oxford University expedition to British Guiana and recorded by Hingston (1932), there seem to be few published accounts of insect behaviour above the canopy of tropical forest. In the Guiana forest, Hingston saw Odonata flying commonly around the crowns of emergent trees at heights of at least 120 feet, and recorded the occasional presence above the canopy of Ephemeroptera, Trichoptera and Chironomidae. He also described considerable activity in the canopy of other groups of insects with which the present paper is not immediately concerned.

Comparative observations which have been made inside and outside rain-forest, both horizontally (Haddow, 1945*a*) and vertically (Part II), indicate that the microclimatic barrier encountered by insects at the forest margin is much the same at ground level and at the top of the canopy, and further that this barrier tends to disappear at sunset. That is, the canopy is to be regarded as presenting a simple forest-edge situation, although perhaps one in which physical environmental factors are somewhat more severe during daytime than they are at ground level. Thus Schimper (quoted by Pittendrigh, 1948) recognised as a distinct community a group of epiphytes which occurred on low bushes of savannah and also at the top of the forest canopy; and Pittendrigh (1948) has shown that certain bromeliads, whose distribution is largely governed by light, occur both in the canopy and also at the forest edge near ground level.

Certain observations recorded here are in accord with this interpretation. During the daytime the insects seen above the canopy were not forest species, but those typically active in fairly open situations at ground level. *Aethriamanta rezia* was making short flights from a sunny perch above the canopy just as it does in a thicket situation near the ground; the aggregations of *Rhyothemis fenestrina* were similar to those which occur outside the forest margin at heights of 10–30 feet; and *Pantala flavescens* was flying across the canopy much as it does at about 10–15 feet over open ground.

At sunset and sunrise, as well as during the night, insects active above the canopy also include those which have come from inside the forest. The situation from which a given insect has come may sometimes be indicated by its vertical distribution, as illustrated here by the Chaoboridae.

The status of the canopy as a marginal site is well demonstrated by the crepuscular behaviour of *Acanthagyna villosa*. Adults rest inside forest or in heavily shaded sites during the day, and come out to feed in exposed places at sunset and

probably also at sunrise. This behaviour has also been observed in two species of the allied genus, *Heliaeshna*, at Zika Forest, near Entebbe, where, at sunset, hawking adults can be seen to be active at the forest edge from ground level to well above the canopy, while during the daytime they rest in deep shade inside the forest. In this connection it is also worth mentioning that the mosquito, *Mansonia metallica*, exhibits swarming activity at sunset both above the canopy (Part V, p. 290) and in open situations only about 8–10 feet above the ground. Thus further investigation may reveal that some of the other insects known to swarm above the canopy in the twilight periods, such as for instance certain Tabanidae (Part V, p. 298) and Ephemeroptera, may also do so in comparable situations near the ground outside forest.

Finally, brief mention should be made of two other findings reported here. The first concerns the capture in light-traps of Anisoptera late at night. There have been many recorded instances of Odonata being attracted to lights (*e.g.* Campos, 1931 ; Wright, 1944), but many have concerned individuals which arrived shortly after sunset, and which could therefore have been engaged in crepuscular feeding activity. At Mpanga, however, where hourly collections were made, we have unequivocal evidence of mature adults of *Orthetrum julia* being active as late as 00–01 hours. It is interesting to note that this dragonfly is also active in sunny situations on the forest floor during the day.

The second finding concerns the utilisation of bamboo sections by ovipositing females of *Hadrothemis camarensis*. Such behaviour is known to occur in dragonflies in the Malaysian Region (Leicester, 1903), where it has been recorded in several species (Lieftinck, 1954) ; but to my knowledge this habit has not previously been reported in any African dragonfly, despite the extensive work which has been undertaken using bamboo sections for mosquito larval surveys in the forests of that continent. Mellanby (1956) found dragonfly larvae in experimental containers in Nigeria, but the receptacles concerned had much wider mouths (internal diameter about 10 inches) than the bamboo sections used here (about 2 inches), and furthermore were outside forest. These observations at Mpanga suggest that *H. camarensis* (like an allied species, *H. coacta* Karsch) typically oviposits in small ground pools on the forest floor, and that this habit has enabled it to utilise uncovered receptacles of water near the ground. It is very unlikely that *H. camarensis* normally breeds in tree-holes, since it is apparently ill-adapted for ovipositing in cavities of small diameter.

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Summary

1. At Mpanga Forest casual observations were made on several groups of insects including Ephemeroptera, Odonata, Trichoptera and Diptera (Chaoboridae and Chironomidae). Observations were made from ground level to a height of 120 feet, about 50 feet above the top of the canopy.

2. Activities described include : swarming (Ephemeroptera, Trichoptera) ; crepuscular feeding (Odonata) ; nocturnal flight (Odonata, Trichoptera, Chaoboridea) ; and oviposition in small containers (Odonata).

3. The observations reported support the view that, from a microclimatic point of view, the canopy is similar to the forest margin near the ground.

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